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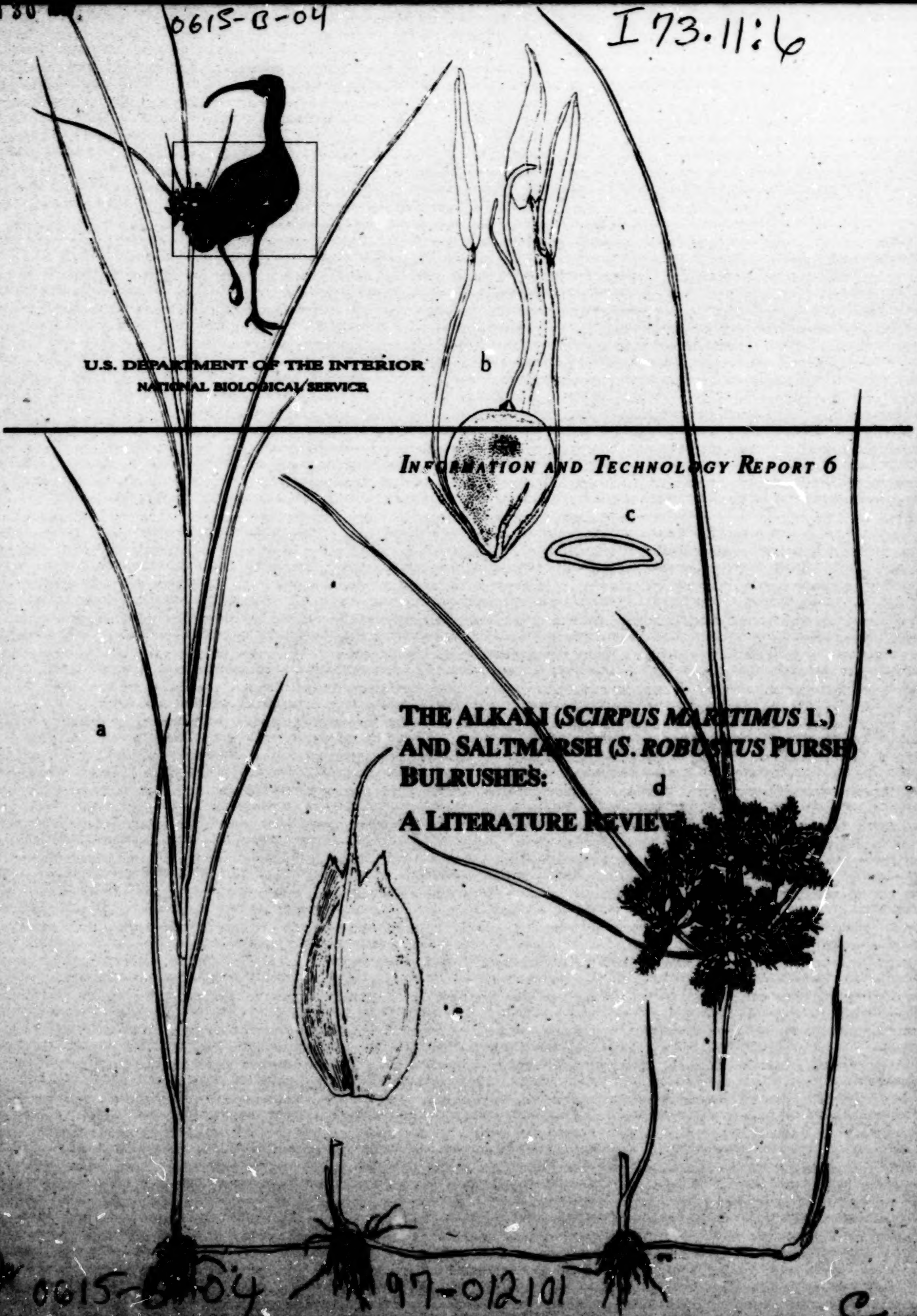
THE ALKALI (*SCIRPUS MARITIMUS* L.) AND SALTMARSH (*S. ROBUSTUS* PURSH) BULRUSHES:

A LITERATURE REVIEW



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SEPTEMBER 1996

THE ALKALI (*SCIRPUS MARITIMUS* L.) AND SALTMARSH (*S. ROBUSTUS* PURSH) BULRUSHES:

A LITERATURE REVIEW

by

Harold A. Kantrud

I

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The Alkali (*Scirpus maritimus* L.) and Saltmarsh (*S. robustus* Pursh) Bulrushes:

A Literature Review

by

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Abstract. Alkali (*Scirpus maritimus* L.) and saltmarsh (*S. robustus* Pursh) bulrushes are closely related, emergent hydrophytes that are important as foods of waterfowl and other wildlife. Water depth, water level fluctuations, exposure, sediment and water salinity, and shading by taller emergents strongly affect growth and reproduction. Important management problems are inconsistent achene germination, difficulties with maintenance and timing of water level and salinity cycles, and acidification of sediments. Other serious problems are competition from other hydrophytes and the largely unpredictable effects of grazing, burning, tilling, and other land use practices. Recent management efforts have focused on thinning stands of the two bulrushes or intermixing them with stands of shorter emergents and submersed plants in order to increase the variety of food plants available to waterfowl and other birds. Information needed for more effective management includes the optimum size and vegetation interspersion of treated areas, treatment response, and the combined effects of natural disturbances such as grazing and burning. Control of a few salt-tolerant plants requires closure of some impoundments to the open sea for long periods. Such closures are of concern to fisheries managers, especially in areas where coastal marshes are disappearing. Conversely, in other managed wetlands, freshwater diverted from rivers pushes estuarine water seaward, making it difficult to obtain waters of sufficient salinity to control undesirable freshwater plants. Research and conservation thus need to be combined in many areas to improve management of these bulrushes.

Key words: Emergent hydrophytes, *Scirpus maritimus*, *Scirpus robustus*, autecology, management, sedges, taxonomy, wetlands, wildlife.

Throughout the world, communities of emergent hydrophytes provide habitat for wildlife. For waterfowl, some of the important communities are dominated by Cyperaceae (sedges), particularly of the genus *Scirpus* (bulrushes). *Scirpus maritimus* and *S. robustus* differ from most bulrushes in that they produce relatively large achenes and carbohydrate-rich corms that are well-known waterfowl foods. Biologists recognize the value of these two bulrushes to waterfowl and other wildlife but seldom differentiate between the species in field studies (Addy 1946; Hyer 1963).

Some authors consider the brackish marsh that supports *S. robustus, S. olneyi (S. americanus)*, and *Spartina patens* the most productive fish and wildlife habitat in the nation (Palmisano 1970). The drastic decline in muskrats (*Ondatra zibethicus*) in Louisiana from the mid-1940's to the mid-1960's is linked to the reduction of *Scirpus robustus* and *S. olneyi* by the more competitive *Spartina patens, S. cynosuroides*, and *Distichlis spicata* (Palmisano and Newsom 1968).

Despite their importance to wildlife, I found no published life histories of *Scirpus maritimus* and *S. robustus*. However, several papers address their phenology, growth, and production as well as the effects of various environmental factors of *S. maritimus* on the species (Hejny 1973; Visperas and Vergara 1976a,b; Lieffers and Shay 1981, 1982a,b; Podlejski 1981, 1982; Dykyjova 1986; Karagatzides and Hutchinson

1991). Other researchers have documented the reproduction, habitat requirements, and management of *S. robustus* (Neely 1960, 1962; Palmisano and Newsom 1968; Mall 1969; Palmisano 1972; George 1980; Prevost and Gresham 1981).

I present here a synthesis of life histories and management assessment of alkali and saltmarsh bulrushes. The information is mostly from reports written in English, from reports with English summaries, and from some foreign material. I did not reference the simple occurrence of either bulrush in various wetlands worldwide or early taxonomic and genetic studies.

Taxonomy and Distribution

by
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Scirpus maritimus L. and *S. robustus* Pursh belong to a small, worldwide group of the family Cyperaceae, in North America often called the "tuberous bulrushes," that needs a taxonomic revision (Wilson 1981; Hulten and Fries 1986; Goetghebeur and Simpson 1991). Taxonomic confusion as reviewed here is due to disagreement about species boundaries, infraspecific variation, misapplication of names, probable hybridization, and introduction of specie[illegible] same name (especially *S. maritimus*) may refer to m[illegible]han one species and to hybrids, and several names are correctly or incorrectly used for the same species. For the references reviewed herein, the names and the species to which they apply therefore must be carefully evaluated.

The group of bulrushes is recognized by perennial rhizomatous habit; large, hard, carbohydrate-rich corms or "tubers" on the rhizomes; leafy, sharply triangular stems; leaflike bracts accompanying the inflorescence; large spikelets; and floral scales that are minutely hairy and apically trifid with prominent midrib extensions ("awns"). Fernald (1950) placed these bulrushes in *Scirpus* section *Phyllantheli* Beurl. and Koyama (1962) called the group the "*Scirpus maritimus* complex." Lye (1971), Haines and Lye (1983), and Strong (1993, 1994) placed the group in the genus *Schoenoplectus.* Other authors (e.g., DeFilipps 1980) treated the group as either *Scirpus* section *Bolboschoenus* Ascherson, or, with the division of *Scirpus* into more natural genera in recent years, segregated the group into the genus *Bolboschoenus* (Aschers.) Palla (e.g., Hejny 1960; Caspar and Krausch 1980; Koyama 1980; Wilson 1981; Browning and Gordon-Gray 1993; Browning et al. 1995). The group will probably be placed in *Bolboschoenus* in an upcoming volume of *Flora of North America* (Flora of North America Editorial Committee. Cyperaceae. Flora of North America north of Mexico. Volume and date to be determined. Oxford University Press, New York, unpublished) in which case the correct names of *S. maritimus* and *S. robustus* will be *Bolboschoenus maritimus* (L.) Palla and *Bolboschoenus robustus* (Pursh) Sojak (S. Galen Smith, Department of Biology, University of Wisconsin-Whitewater, Whitewater, Wisconsin, personal communication).

For North America, recent taxonomists (Beetle 1942; Fernald 1943, 1950; Koyama 1962; Schuyler 1975; Browning et al. 1995) have interpreted species boundaries variously. Browning et al. (1995) provided several new diagnostic characters using scanning electron microscopy of achenes and argued that hybridization where the species grow together is responsible for much of the taxonomic confusion in this group (see especially *Scirpus novae-angliae* and *S. glaucus* below). We herein recognize the following five species for North America: *S. maritimus* L., *S. robustus* Pursh, *S. fluviatilis* (Torr.) Gray, *S. novae-angliae* Britt., and *S. glaucus* Lamarck (introduced from the Old World). For North American synonymy we mostly follow Kartesz (1994).

We treat *S. maritimus* as "s. lat." ("*sensu lato*", or "in a broad sense") pending further studies because the species is very difficult to delimit and is treated as s. lat. in much of the ecological literature. For North America and Hawaii, some authors (e.g., Beetle 1942; Fernald 1950; Schuyler 1975) segregated most plants of *S. maritimus* into *S. paludosus* A. Nelson, while others, especially recently (e.g., Gleason 1952; Koyama 1962, 1990; Gleason and Cronquist 1963, 1991; Hitchcock et al. 1969; Cronquist et al. 1977; Scoggan 1978; Boivin 1992; Smith et al. 1993; Kartesz 1994; Browning et al. 1995) treated *S. paludosus* as a synonym, variety, or subspecies of *S. maritimus*. Synonyms of *S. maritimus* L. for North America as herein treated are: *Scirpus brittonianus* Piper; *S. campestris* Britt.; *S. fernaldii* Bickn.; *S. interior* Britt.; *S. maritimus* var. *fernaldii* (Bickn.) Beetle; *S. maritimus* var. *paludosus* (A. Nelson) Kuek.; *S. pacificus* Britt.; *S. paludosus* A. Nelson; *S. paludosus* A. Nelson var. *atlanticus* Fern.; *S. robustus* var. *campactus* Davy ex Jepson; *S. robustus* Pursh var. *paludosus* (A. Nelson) Fern.; *Bolboschoenus maritimus* (L.) Palla; *B. maritimus* (L.) Palla subsp. *paludosus* (A. Nelson) T.

Koyama; *B. paludosus* (A. Nels.) Soo; *Schoenoplectus maritimus* (L.) K. Lye.

For Europe, most recent taxonomists have recognized only *Scirpus maritimus* but with various subspecies, varieties, and forms (e.g., Suessenguth 1939; Schultze-Motel 1980; Hulten 1964; Hulten and Fries 1986). Some taxa reportedly occur variously in alkaline or acid fresh waters or in waters of greater or lesser salinity (Hejny 1960; Robertus-Koster 1969; Caspar and Krausch 1980). Norlindh (1972) and Dykyjova (1986) reviewed the taxonomy and biogeography of *S. maritimus* s. lat. in Eurasia. For *Flora Europaea*, DeFilipps (1980) followed Nordlindh (1972) in recognizing only *S. maritimus*, placing *S. compactus* Hoffm. in synonymy, and treating the mostly Asian *S. affinis* Roth as *S. maritimus* subsp. *affinis* (Roth) Nordlindh. In addition, recent work has shown that *S. yagara* Ohwi (*S. fluviatilis* subsp. *yagara* [Ohwi] Koyama) and probable *S. maritimus* × *yagara* hybrids occur in Europe and are probably included within the concept of *S. maritimus* there (Browning et al. 1996).

For eastern Asia, Koyama (1958, 1980) recognized three taxa: *S. maritimus, S. fluviatilis* subsp. *yagara*, and *S. planiculmis;* he also showed that most plants previously called *S. planiculmis* F. Schmidt belong in *S. maritimus* and that the true *S. planiculmis* is a very different Pacific coastal endemic. For Australia, New Zealand, and various southern Pacific islands, taxonomists (e.g., Cook 1947; Wilson 1981) recognize the three species: *S. caldwellii* V. J. Cook, *S. medianus* V. J. Cook, and *S. fluviatilis.* The latter species is also North American. For southern Africa and elsewhere, Browning and Gordon-Gray (1993), Smith (1995), and Browning et al. (1995) showed that *S. maritimus* s. lat. as previously treated includes *S. glaucus* Lamarck and probable hybrids (see following sections).

Taxonomists have generally treated trigynous plants (with trifid styles and trigonous achenes) as "typical" *S. maritimus* (e.g., Ascherson and Graebner 1902-1904; Fernald 1943, 1950; Koyama 1958; Gleason 1952, 1963; Robertus-Koster 1969; Nordlindh 1972; Caspar and Krausch 1980; Boivin 1992) and have placed digynous plants (with bifid styles and lenticular achenes) in various infraspecific taxa such as *S. maritimus* var. *digynus* Godron or in separate species such as *S. paludosus* A. Nels., *S. affinis* Roth, *S. compactus* Hoffmann, and *S. planiculmis* F. Schmidt (misapplied). Trigynous plants are common in Europe and southern Africa but rare in North America (Browning et al. 1995).

Scirpus maritimus and *S. robustus* differ by very few achene and other characters (e.g., Schuyler 1975; Browning et al. 1995). These species have been confused by several authors, especially on the Pacific coast; for example, Mason (1957), Munz and Keck (1959), and George (1963) erroneously placed *S. maritimus* in synonymy under *S. robustus.* Correll and Correll (1975) treated *S. robustus* under its synonym *S. maritimus* var. *macrostachyus* Michx. These two bulrushes are especially variable in their zones of sympatry on the northern Atlantic coast as described by Fernald (1943) and Schuyler (1975) and in California (S. G. Smith, unpublished). Some of this variation is the basis for infraspecific taxa recognized by, for example, Fernald (1943, 1950) and Hulten and Fries (1986). Browning et al. (1995) ascribe much of this variation to hybridization. Synonyms of *S. robustus* are *Bolboschoenus robustus* (Pursh) Sojak and *Scirpus maritimus* L. var. *macrostachyus* Michx.

Scirpus novae-angliae, known only from northern Atlantic coastal estuaries, is controversial. Beetle (1942), Gleason (1952), and Gleason and Cronquist (1963) placed this bulrush in *S. robustus,* while Fernald (1950) and Koyama (1962) placed it in *S. maritimus.* Koyama (1962) reduced *S. novae-angliae* to var. *cylindricus* (Torr.) T. Koyama of the unrelated *S. subterminalis* Torrey. Schuyler (1975), under *S. cylindricus,* clarified the nomenclature of *S. novae-angliae* and described its morphology and habitat, and Ferren and Schuyler (1980) further described its habitat. Browning et al. (1995) argued that *S. novae-angliae* originated as *S. fluviatilis* × *robustus* hybrids because it: (1) is morphologically intermediate; (2) grows in habitats intermediate between the saline habitats of *S. maritimus* and *S. robustus* and the freshwater habitats of *S. fluviatilis;* and (3) is known almost only from the zone of sympatry of its putative parents. Synonyms of *S. novae-angliae* are: *S. campestris* var. *novae-angliae* (Britt.) Fern.; *S. maritimus* var. *cylindricus* Torr.; *S. robustus* Pursh var. *novae-angliae* Beetle; *S. cylindricus* (Torr.) Britt.; *S. subterminalis* Torr. var. *cylindricus* (Torr.) T. Koyama; *Bolboschoenus novae-angliae* (Britt.) S. G. Smith; and *Schoenoplectus novae-angliae* (Britt.) M. T. Strong.

Beetle (1942), Mason (1957), George (1963), Munz and Keck (1959, 1973), and Smith et al. (1993) also included a species that they called *Scirpus tuberosus* Desf. Koyama (1962) reduced this species to *S. maritimus* var. *tuberosus* (Desf.) T. Koyama. Smith (1995), however, showed that the name *S. tuberosus* Desf. is a synonym of *S. maritimus,* and that *S. glaucus* Lamarck (*Bolboschoenus glaucus* [Lam.] S. G. Smith) is a correct name for this species. Browning et al. (1995) showed that *S. glaucus* and *S. maritimus* differ greatly in their achene structure, and that many specimens from wildlife refuges, rice fields, and waste sites in California are probably *S. glaucus* × *maritimus* hybrids. *Scirpus glaucus* is widespread in Asia and Africa, where it is often included in the concept of *S. maritimus* (Browning et al. 1995 and personal communication). *Scirpus glaucus* was introduced into North America, where it is definitely known from California, Oregon, Idaho, and New York (S. G. Smith, unpublished).

Below we list the common or colloquial names that have been applied to *S. maritimus* and *S. robustus*, but possibly erroneously to other closely related species as reviewed above. Besides alkali bulrush (Scott and Wasser 1980), *S. maritimus* is locally known as bayonet grass, perennial nutsedge, prairie bulrush, purua grass, saltmarsh bulrush, sea club-rush, seacoast bulrush, and tule (Wetmore 1921; Christensen et al. 1947; Fernald 1950; Hyer 1963; Batten 1967; Nakagawa et al. 1973; Kim and De Datta 1974; Yamanaka 1975). Scott and Wasser (1980) prefer the common name saltmarsh bulrush for *S. robustus*. Others call the plant buttergrass, coco, goose grass, leafy three-cornered grass, leafy three-cornered rush, leafy sedge, leafy three square, leafy three-cornered sedge, nut grass, robust bulrush, saltmeadow bulrush, sea club rush, stout bulrush, triangle sedge, and wild chufa (McAtee 1939; Lay and O'Neil 1942; Lynch et al. 1947; O'Neil 1949; Brown 1959; Beter 1957; Kimble 1958; Linthurst and Seneca 1980; Hackney and Cruz 1982; Payne 1992; Anonymous 1994).

Chromosome numbers reported for *S. maritimus* worldwide vary from approximately n=40-57 (2n = 80-114) as summarized by Chapman (1974) and Cronquist et al. (1977), and for *S. robustus* in Massachusetts, n= approximately 53-55 (Hicks 1928). Although these reports demonstrate that aneuploid series occur in this complex, chromosome numbers cannot be definitely assigned to species because the taxonomy is so confused as reviewed above and identifications must be confirmed by study of voucher specimens.

Scirpus maritimus s. lat. is one of the most widely distributed plants of the Northern Hemisphere. The species is more or less circumpolar in boreal and temperate regions on coasts and in the interior (Hulten 1964; Ranwell 1972; Koyama 1980; Hulten and Fries 1986) and ascends to at least 3,000 m in Tibet and 2,900 m in Colorado (Hulten 1964). In Europe, *S. maritimus* ranges from just above the Arctic Circle on Russia's Kola Peninsula south to the Mediterranean region. This bulrush occurs in much of North America from about 62° N in Alaska's Cook Inlet area and Northwest Territories, to approximately 55° N on James Bay (where disjunct; Riley and McKay 1980), to about 51° N on the Atlantic coast in Quebec and south to Mexico. *Scirpus maritimus* is absent from the Atlantic coast south of New Jersey and from the gulf coast, except possibly for a small area in Texas. This species is an important member of the Pacific coastal marshes between 35° N and 55° N (Macdonald 1977; Hutchinson 1986). In the interior, *S. maritimus* occurs in saline places rarely in the East and commonly in the West, south to Missouri and Mexico.

Elsewhere, *S. maritimus* occurs in Mexico (Saunders and Saunders 1981) and the Hawaiian Islands (Koyama 1990) and is local in South America (West 1977; S. G. Smith and J. Browning, unpublished) and Africa (Browning et al. 1995 and unpublished). Reports of *S. maritimus* from the southern Pacific (Australia, New Zealand, Tasmania, New Caledonia, etc.; e.g., Congdon 1981) and from the Philippines and New Guinea (e.g., Kern 1974; Kim and De Datta 1974) may refer to *S. caldwellii* V. J. Cook and other species. Many reports of *S. maritimus* and *S. tuberosus* from various warm parts of the Old World, especially in the Middle East, Asia and Africa, may refer to *S. glaucus* Lam. (Browning et al. 1995 and unpublished).

Scirpus robustus Pursh is definitely known only from saline places at low elevations on or near the coasts of North and South America and the Caribbean (S. G. Smith, unpublished). In North America, this species occurs in the East along most of the Atlantic and gulf coasts from New Brunswick and Prince Edward Island to northern Mexico. According to Shisler (1990), *S. robustus* is especially common south of Delaware. On the Pacific coast this bulrush is common in the San Francisco Bay region and very local north to Washington and south to Baja California (Smith et al. 1993; S. G. Smith, unpublished). The distributions of *S. robustus* and *S. maritimus* overlap along the northeast Atlantic coast, on the Pacific coast, and in a small region near the gulf coast of Texas (S. G. Smith, unpublished).

Autecological Classification

Scirpus maritimus and *S. robustus* are perennial emergent macrophytes that reproduce sexually and vegetatively. Lacking salt glands, succulence, and other adaptations of true halophytes, *S. maritimus* and probably *S. robustus* are facultative halophytes that show decreased growth and reproduction in increasingly saline environments yet may persist for centuries in nonsaline habitats (Arnold 1955; Ranwell 1972; Ustin 1984; Kruger and Kirst 1991). These bulrushes are best considered brackish water species that are adapted to flourish at salinities that cause high mortality in freshwater plants yet are able to survive in environments where halophytes dominate.

Investigators often place *S. maritimus* and *S. robustus* into categories based on water salinity (Olsen 1950; Van D[illegible]elarr et al. 1961; Chabreck 1972; Stewart and Kantrud 1972). However, both species occupy habitats in which salinities fluctuate greatly (Dodd and Coupland 1966a; Palmisano 1970; Pearcy et al. 1982). Both species have mechanisms that allow rapid growth and invasion of bare areas when environmental conditions are favorable and increased survival of reproductive material when conditions are stressful (Palmisano and Newsom 1968; Mercado et al. 1971; Lieffers and Shay 1981; Pearcy and Ustin 1984; Dykyjova 1986; Shay and Shay 1986; Karagatzides and Hutchinson 1991). *Scirpus maritimus* is one of the few species able to invade established stands of the hybrid *Spartina anglica* in coastal Europe (Beeftink 1985). In contrast, population sizes of both bulrushes often decrease or disappear in a few years as taller plants flourish after fires or after the cessation of grazing (Beter 1957; Duncan and D'Herbes 1982). Both bulrushes are indicators of disturbance (Beeftink 1966; Palmisano 1970; Pederson and Van der Valk 1984) and rapidly invade bare mudflats (Dahl and Hadac 1941, cited in Chapman 1974; Wilkinson 1970; Flowers 1973; Eilers 1975; Moody 1978; Hutchinson 1982).

Physiologists classify *S. maritimus* as a C_3 plant (i.e., it fixes CO_2 directly into a three-carbon molecule), and its net rate of photosynthesis is much below maximal (Rozema et al. 1991). Aerenchymatic tissue develops well in the belowground parts (Tyler 1969). Rhizomes can produce new shoot growth under 2 months of continuous anaerobic incubation and can survive nearly 3 months of anoxia (Barclay and Crawford 1982, 1983; Braendle and Crawford 1987). However, seedlings grown in detritus collected from established stands may show poor growth in anoxic environments (Clevering and Van der Putten 1995). *Scirpus maritimus* is able to exclude mineral salts while accumulating sugars and other photosynthetic products for osmotic adjustment (Ustin 1984). Reciprocal transplant experiments suggest that this bulrush has little local genetic adaptation and that plants adjust shoot height, mass, density, and flowering frequency to their environment (Karagatzides and Hutchinson 1991).

Devotees of the European Zurich-Montpellier (Z-M) school of phytosociology (Braun-Blanquet 1932) place communities dominated by *S. maritimus* in a hierarchical system of classes, orders, federations, associations, and subassociations. For example, the federation *Bolboschoenion maritimi* Dahl & Hadac 1941 occurs in the littoral zones of Czechoslovakian fish ponds (Hejny and Husak 1978) and the association *Bolboschoenetum maritimi* Van Langendonck 1931 occurs in coastal Norway (Vevle 1985). *Scirpus maritimus* also occurs as a nodum in the alliance *Phragmition* in British salt marshes (Adam 1981) and as a companion or differential species in many salt marsh communities in coastal Europe (Westhoff 1979). North American phytosociologists seldom follow the Z-M school. An exception is Looman's (1981) classification of saline areas of the Canadian prairie provinces, where *S. maritimus* was represented in six of eight associations and was the dominant species in one association.

Development and Reproduction

Except where specific references are given, the information in this section is from the sources in Table 1 and standard botanical texts.

Belowground Parts

The main belowground parts of *Scirpus maritimus* and *S. robustus* are roots, rhizomes (horizontal stems often called **stolons**) and corms (enlarged stem bases often called **tubers**; Fig. 1). No rooting material of either species occurs more than 60 cm belowground. In nature, the bulk of the belowground biomass of *S. maritimus* probably occurs within 20 cm of the surface (Fiala et al. 1968), but corms can form at 30-40 cm depth in culture. McNease and Glasgow (1970) found more than 98% of the rhizome mass of *S. robustus* less than 11 cm belowground and none at depths exceeding 18 cm. *Scirpus maritimus* rhizomes are white and thin and seldom exceed 4% of the plant mass. Shoots, roots, and corms form at nodes (joints) along the rhizomes that are usually unbranched. The internodal length of *S. maritimus* is usually about 4-12 cm (rarely as long as 20 cm). Smaller corms are sometimes adnate to a larger mother corm. These thick (as wide as 3 cm), ligneous, and scaly structures are creamy white when young but soon turn brown and finally black. The dry weight of an *S. maritimus* corm may exceed 0.5 g and may account for 60% or more of the plant mass. Each corm has 1-5 buds that can grow or assume dormancy. Corm growth can lead to more corms or adventitious shoots (tillers). In *S. maritimus*, as many as 45 tillers may develop in one season from a single overwintered corm. Living roots of both bulrushes are tan to orange and rigid, whereas dead roots are brown or black and flaccid. The maximum

Table 1. References and subject material about the morphology and reproduction of *Scirpus maritimus* or *S. robustus*.

Reference	Subjects covered
Knuth 1899, cited in Leereveld et al. 1981	Flower maturation
Bicknell 1901	Phenology and morphology
Praeger 1913, cited in Chapman 1974	Achene buoyancy
Wetmore 1921	Morphology, achene retention
Isely 1944	Germination tests, achene stucture
Olsen 1945	Flowering rate
Christensen et al. 1947	Morphology, achene weights
Lynch et al. 1947	Achene viability
Neely 1960	Achene dispersal
Kaushik 1963	Germination requirements
Bolen 1964	Phenology
Ungar 1965	Phenology
DeVlaming and Proctor 1968	Achene retention in birds
Palmisano 1967	Achene germination and dispersal, morphology, phenology
Palmisano and Newsom 1968	Achene germination
Mall 1969	Phenology
Burgess 1970	Achene volume
McNease and Glasgow 1970	Rhizome depth
Palmisano 1970	Achene germination, corm growth
Ghosh 1971, cited in Mercado et al. 1971	Growth rate
Lye 1971	Embryo morphology
Mercado et al. 1971	Salinity effects on corm germination
Dykyjova et al. 1972	Tiller development
Palmisano 1972	Effects of salinity on achene germination
Dykyjova 1971	Morphology
Daiber 1974	Avian achene dispersal
Flowers and Shontz 1974	Germination ecology
Kim and De Datta 1974	Corm morphology and germination
Dykyjova and Pribil 1975	Growth rate
Eilers 1975	Phenology
Visperas and Vergara 1976a	Growth characteristics
Visperas and Vergara 1976b	Effects of light and temperature on flowering and corm production
Dietert and Shontz 1978	Germination ecology
Heitzman 1978	Morphology, phenology
Husak and Hejny 1978	Flowering
Moody 1978	Proportion of reproductive stems
Drifmeyer and Zieman 1979	Achene germination, allelopathy
Congdon 1981	Clone expansion
Lieffers and Shay 1981	Effects of water levels on reproductive strategy
Pomeroy et al. 1981	Shoot density
Prevost and Gresham 1981	Achene weights
Smith and Odum 1981	Root descriptions
Lieffers and Shay 1982a	Phenology
Lieffers and Shay 1982b	Morphology, germination
Pearcy et al. 1982	Corm dormancy
Podlejski 1981, 1982	Phenology, morphology
Ustin et al. 1982	Phenology, corm dormancy
Pederson 1983	Achene dispersal and distribution
Smith, L. 1983	Phenology, effects of burning on achenes in seed bank
Smith and Kadlec 1983	Effects of drawdown on achene germination
Pederson and van der Valk 1984	Achene dispersal, seed bank studies
Krisch 1985	Proportion of reproductive stems, shoot weights
Smith and Kadlec 1985a,b	Effects of disturbance on seed banks, germination tests, achene dispersal
Dykyjova 1986	Phenology, morphology
Krisch 1986	Phenology, growth rate
Brandle and Crawford 1987	Corm survival under anoxia
Foote 1988	Achene resuspension
Hall and Yesaki 1988	Shoot growth
Karagatzides and Hutchinson 1991	Phenology, biomass allocation, vegetative and sexual reproductive effort
Browning and Gordon-Gray 1992, 1993	Achene morphology
Clevering 1995	Germination and seedling emergence

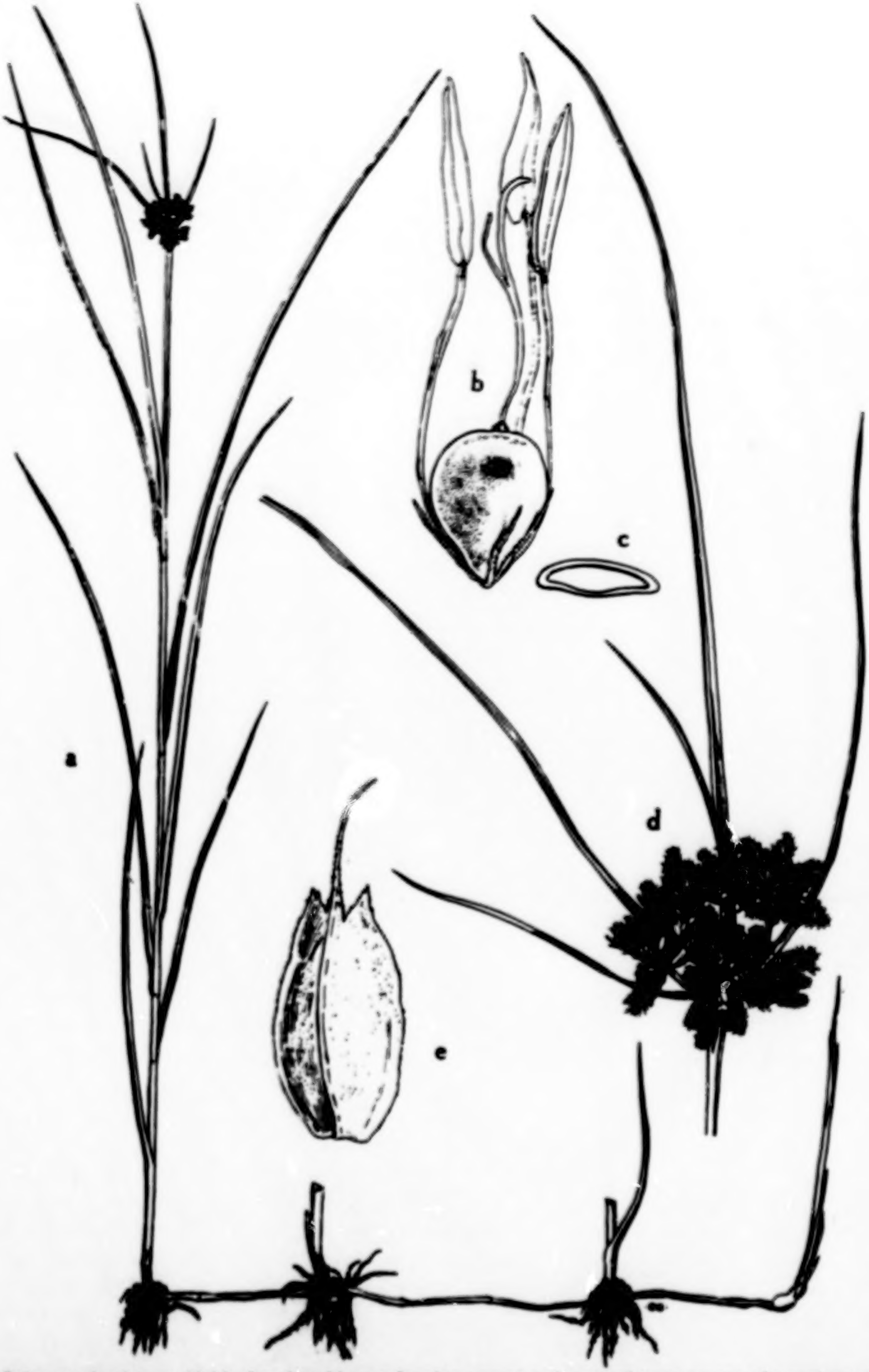

Fig. 1. *Scirpus robustus*. a. Habit showing rhizome-forming corms and general appearance of a mature plant, x 0.16; b. lens-shaped achene showing anthers, stigma, and bristles, x 7.6; c. cross section of achene, x 7.6; d. inflorescence, showing involucral leaves, x 2.0; e. awned scale, x 4.9. Appearance of *S. maritimus* is similar. (From Mason 1957; reproduced with permission of University of California Press, Berkeley.)

root length of North Dakota specimens of *S. maritimus* is about 10 cm (personal observation).

Aboveground Parts

Scirpus maritimus and *S. robustus* attain heights of about 1.5 m, but the average is much less and can be as little as 8 cm in dry or heavily grazed stands. During peak growth periods, stems elongate at about 1-3 cm/day. Reproductive stems can be twice as tall as vegetative stems. The dry weight of a mature stem is about 1-5 g. Reproductive stems usually compose about 20-75% of the total stems when maximum standing crop is attained.

Scirpus robustus has as many as nine stem leaves, *S. maritimus* as many as 13; leaves of both species are as much as 60 cm long and 1.5 cm wide. Leaves of *S. robustus* can grow 3.8 cm/day in the laboratory. As many as four leaflike bracts attach below the inflorescence. The inflorescence consists of one to several ovoid to lanceolate spikelets, 1-4 cm long, sessile and clustered or some on the tips of rays (Fig. 1). Dry *S. maritimus* inflorescences weigh as much as 1.03 g, usually less than 2% of the total plant mass. In *S. maritimus* (and probably *S. robustus*) the stigmas mature before the anthers. Seedlings of both bulrushes probably do not flower in the first year, at least not in temperate regions.

Spikelets of mature plants produce as many as 25 olive to black, one-seeded, indehiscent fruits called achenes. These are shiny, flattish to lens-shaped or with a low angle on the back. They are as much as 0.4 cm long and have an apiculate tip that represents the persistent style base. The volume of a single *S. maritimus* achene is about 0.004 ml; the air-dried weight is about 5.6 mg. Air-dried *S. robustus* achenes weigh about 3.3 mg and fresh achenes about 3.5 mg. Isely (1944), Koyama (1962), Schuyler (1975), Browning and Gordon-Gray (1992, 1993), and Browning et al. (1995) provide additional information on spikelet, achene, and embryo morphology of *S. maritimus*, *S. robustus*, and related species.

Phenology

Phases in the growth of established stands of *S. maritimus*, from the beginning to the end of the growing season, are as described by Dykyjova et al. (1972): (1) shoots use energy reserves stored in corms; (2) belowground parts grow after aboveground growth is well developed; (3) generative organs form when aboveground biomass is maximum; (4) organic substances translocate to belowground parts at senescence.

In northern California and in the Pacific Northwest, *S. robustus* and *S. maritimus* show winter dormancy, new shoot growth from corms in March and April, flowering in May, peak growth rate in June or July, and peak shoot mass in August or September. However, New York populations of *S. robustus* sometimes do not flower until mid-June, nearly 1 month later than *S. maritimus*. Louisiana populations of *S. robustus* also are dormant in winter, begin spring growth when soil temperatures exceed 16° C, flower in mid-April, and maturate achenes in late August. The initial growth of *S. maritimus* in Utah begins in early to mid-April; anthesis is in early May. In Kansas, *S. maritimus* flowers from May through July and fruits from June through August. Saskatchewan plants begin growth from corms in May, the first shoots flower in June, the second nonflowering shoots mature by late August, and all aboveground parts are dead by October. In southern France, *S. maritimus* is dormant from October to January, at which time the underground buds begin growth. Shoots appear in February, and in early March buds destined to become rhizomes appear. The underground network is well developed by the end of April, flowering starts in mid-May or early June, and fruiting begins at the end of June or in early July. In Czechoslovakian fish ponds, *S. maritimus* sprouts corms at the beginning of May, flowers by late June, and ripens achenes by the end of August; peak biomass occurs after 86-94 days of growth. In Baltic populations of *S. maritimus*, new stems are evident by the end of April; flowering occurs in late May, and stems are dead by late July or early August.

Sexual Reproduction

I assume that alkali and saltmarsh bulrushes are wind-pollinated. *Scirpus maritimus* pollen is eaten by some syrphid flies, but it is unknown whether these flies are effective pollinators (Leereveld et al. 1981; Leereveld 1984).

Achene germination and seedling growth are relatively rare events in mature, natural stands of *S. maritimus* and *S. robustus*; sexual reproduction mostly serves to spread plants to new areas. In general, plants shift energy to achene production when water becomes deeper and salt concentrations decrease. Achene production may depend on energy stored in corms during prior years. Achenes of both species initially float and eventually sink and overwinter on or under submersed sediments. *Scirpus maritimus* achenes sometimes overwinter in the spikelets and shed gradually until spring.

The achenes of both bulrushes float for longer periods than do propagules of many other hydrophytes.

Scirpus maritimus achenes float for as long as 4 weeks and those of *S. robustus* for more than 4 months. The floating achenes of both species disperse, primarily from winds or currents, to shores or shallow vegetated areas. Dispersal by birds probably is common. Feeding trials show that the viability of *S. maritimus* achenes is enhanced in the intestinal tracts of killdeers (*Charadrius vociferus*) and mallards (*Anas platyrhynchos*), where retention times average about 4 and 2 days, respectively.

After sinking, the achenes are viable for at least 2 years. Achenes can be abundant in sediments supporting submersed hydrophytes (Grillas et al. 1993), but few occur in the deeper areas of large wetlands. Nearly all achenes are in the upper 6 cm of bottom sediments. Achenes from previous growing seasons can be resuspended by wave action (Foote 1988). Achenes sometimes are well represented in seed banks, even when plants do not occur in existing vegetation.

Achenes germinate under conditions of relatively high illumination and temperature and low salinity in shallow water or on exposed saturated bottoms. *Scirpus robustus* achenes can germinate while floating. Roots emerge only when seedlings are in contact with bottom substrates.

The germination requirements of *S. maritimus* and *S. robustus* achenes are well known (see later section on propagation). *Scirpus maritimus* achenes germinate poorly at maturity, but 97% germination can be obtained 2 months later. *Scirpus robustus* achenes collected late in the growing season and stored in air-tight containers for more than 5 years readily germinate. Regardless of age, achenes held at a constant 2-4° C germinate at higher rates. Such after-ripening and stratification occur naturally in wetlands during the winter after production. Ninety percent germination of *S. robustus* achenes can be obtained in commercial germinators set for a daily cycle of 14 h of light at 35° C and 10 h of dark at 20° C. Germination begins in 7 days and can continue for 30 days. Pericarp injury by mechanical means or by acid treatments increases germination. Germination requires light yet seems little affected by photoperiod length. Darkness may induce a secondary dormancy in *S. robustus* achenes that may prevent their germination when buried or when exposed in heavy shade.

Germination of achenes of both bulrushes increases with increasing daytime temperatures and when temperatures fluctuate. Regardless of storage conditions, *S. robustus* achenes subject to alternate freezing and thawing or constant freezing germinate better than those stored at room temperature. Optimum temperatures for *S. robustus* germination are 35° C during day and 25° C at night. For *S. maritimus*, optimums are 25-35° C during the day and at least 5° C lower at night.

Under proper light and temperature cycles, *S. robustus* achenes show high germination rates on paper moistened with distilled water. Even small amounts of salts depress germination and seedling growth. Germination is reduced by about half when the paper is moistened with water of 9-15 g/L salinity and is nil when salinity is more than 21 g/L. *Scirpus maritimus* achenes may continue to germinate at slightly higher salinity levels. Salinity probably reduces germination by reducing water absorption by the achenes. Salinity reduces the speed as well as the percentage germination of *S. maritimus* achenes. No chemicals found in other hydrophytes are known to significantly depress achene germination in either of the two bulrushes.

Achenes of the two bulrushes may differ in moisture required for germination. As little as 2.5 cm of water over *S. robustus* achenes held in pure quartz sand stifles germination for at least 25 days, but the same achenes germinate normally when water levels are lowered to the sand surface. However, more *S. maritimus* seedlings emerge when core samples of bottom substrate are held under 4-5 cm of water than when they are merely kept moist, although the germination rate is highest when these conditions alternate. For this species, water depths of less than 10 cm have little effect on germination of achenes buried 2 cm or less in sediments.

In summary, both bulrushes have adaptations for achene production, dissemination, and germination in unstable environments where water levels and salinities fluctuate and bottom sediments are exposed.

Asexual Reproduction

The common mode of expansion of clones of *Scirpus maritimus* and *S. robustus* is by a network of creeping rhizomes and corms that are concentrated at the periphery. After the dormant period, shoots and tillers initially grow from the old corms; several weeks later buds destined to become rhizomes appear. Rhizomes grow in a linear pattern and bear new shoots at regular intervals. Little, if any, seedling production occurs inside an established network of rhizomes. Clones of *S. maritimus* can expand vegetatively as fast as 2 m/year and attain a diameter of 24 m. The vegetative life cycle of this species is about 130 days. The central portions of older annular clones often die and expose corms, roots, and rhizomes. If competition from other plants is not severe, rhizomes of *S. robustus* can gain 5.2 g/day live weight, grow 2.1 cm/day, and add 0.2 nodes/day during peak growing periods. This species also reproduces from rhizome fragments if adequate growing conditions occur within 5 months; whether *S. maritimus* has this ability is unknown.

A substantial amount of the current-year growth of both bulrushes depends on the carbohydrate-rich corms that can remain dormant under conditions of low water levels and high salinity for at least 2 years. Germination of *S. maritimus* corms is inhibited when moisture content falls below 16% or sediment surfaces remain dry for about 1 month (Cao 1974, cited in Vergara et al. 1977). *Scirpus maritimus* exhibits bud dormancy whereby some of the usually 1-5 buds can remain dormant when the corms first germinate. Like achene germination, corm sprouting and growth are negatively affected by increased water salinity. The upper salinity limit for sprouting of *S. robustus* corms is about 21-30 g/L.

Physiology

Salinity reduces achene germination and corm sprouting in *Scirpus maritimus* and *S. robustus*. High salinity also reduces overall growth rate, culm height and diameter, root development, number of leaves, and other growth measures (Kaushik 1963; Palmisano 1970). Physiologists provide further evidence that *S. maritimus* is not a true halophyte. Ranwell (1972) classified *S. maritimus* as a facultative halophyte, citing work by Arnold (1955) showing that the plant does not develop sufficient cell-sap pressure to survive the salinity of full-strength seawater. Kruger and Kirst (1991) further classified *S. maritimus* as a facultative halophyte of the accumulating type because plants from both oligohaline and mesohaline sites show no indication of morphological adaptations to salt tolerance but do accumulate sodium and chlorine ions. Plants from mesohaline sites show constant increases in osmotic potential of the cell sap during the growing season and accumulate sodium and chlorine ions until leaves begin to die. Levitt (1980) also noted accumulation of sodium and chloride as an osmotic adaptation in *S. maritimus*. The leaves of this species do, however, have at least six adaptations of the stomata, epidermis, parenchyma, and sclerenchyma that may enhance survival under saline conditions (Mateu 1991).

Moderate salinities may benefit *S. maritimus*. In studies of Mercado et al. (1971), young plants grown under increasing sodium chloride concentrations (as much as about 7 mS/cm in the soil extract), generally produced larger plants, more shoots, and more big corms per plant than plants grown in fresher water (1.4-4.6 mS/cm). Mercado et al. (1971) considered the plant a salt lover, albeit not a true halophyte whose existence depends on saline habitat. Similarly, Kaushik (1963) showed that *S. maritimus* plants cultured in water of about 5.8 g/L salinity produce more achenes than plants grown at lower salinities. He listed symptoms of excessive salinity that appear in plants when salinities are raised to about 7.7 g/L. These include necrotic mottling and chlorosis (yellowing) of leaves, pale green color, curling and discoloration of leaf tips, dwarfing, and reduced root and root-hair development. Except for chlorosis and dwarfing, these symptoms are less evident in plants grown outdoors (Kaushik1963).

Concentrations of chlorine and sodium ions in culms and roots of *S. robustus* reflect the levels in the root zone, but when levels there are very low, plants concentrate these ions in culms and roots (Palmisano 1970). The effects of salinity on the physiology of *S. robustus* were investigated more thoroughly by Pearcy et al. (1982) and Pearcy and Ustin (1984). Relative growth rate is more strongly inhibited than photosynthesis, even at moderate (10 g/L) salinities, and may be a primary factor decreasing productivity in saline habitats. Productivity is more restricted by reduced photosynthetic leaf area than by decreased rates of photosynthesis. Plants increase allocations to belowground structures and reduce rates of leaf elongation and leaf length at high salinities. Plants exclude mineral salts and use organic compounds for osmotic adjustment. These adaptations to high salinities may be less efficient than those possessed by true halophytes. However, *S. robustus* may have greater salt tolerance than indicated by indoor culture experiments because plants can attain large leaf areas early in the growing season when water salinities are lower. The timing of salinity stress is important. Plants that develop under lower salinity but whose growth is curtailed by higher salinity later in the season may still shade out possible competitors.

Methods of osmoregulation in 16 European halophytic angiosperms were studied by Briens and Larher (1982). *Scirpus maritimus* was included in a group of emergent species that accumulate little water and low concentrations of inorganic ions in the shoots and relatively large amounts of water in the roots. Soluble carbohydrates, especially sucrose, found in relatively large amounts in the leaves and rhizomes, seem to be the organic solutes that have significant osmotic function in this plant. The carbohydrate reserves are probably also responsible for the ability of the buried rhizomes of this species to survive long periods of anoxia and still send shoots through to the surface (Barclay and Crawford 1982). Clevering et al. (1995) found that during the period of submerged growth, *S. maritimus* can take up ample oxygen from the water. They also found that during this period relative growth rate is independently affected by light availability and corm size. After this period, plants grown from small corms (8.9 + 2.6 g fresh weight) in darkness can weigh only 67% of plants grown from large corms (16.2 + 2.8 g fresh weight). Whether or not carbohydrate accumulations are involved in the selection of these plant parts by feeding waterfowl is unknown. In *S. maritimus*, the concentration of the amino acid proline seems too small to serve as a cytoplasmic osmoticum (Popp and Albert 1980).

Higher average temperatures generally produce taller plants and favor shoot and corm production in *S. maritimus* (Visperas and Vergara 1976b). The optimum indoor air temperature range for maximum CO_2 uptake in *S. robustus* is 27-32° C; at 20° C, the plant has higher rates than three other associated hydrophytes (Pearcy et al. 1982). The photosynthetic rate peaks at leaf temperatures of about 30° C. Plants survive in high-salinity California wetlands by completing vegetative growth in spring when temperatures are cool and salinities low (Pearcy and Ustin 1984).

Scirpus maritimus produces taller plants with fewer shoots and corms under longer photoperiods, but photoperiod has no effect on flowering; low light intensity drastically reduces growth and production of shoots and corms (Visperas and Vergara 1976b). High light intensity (2,000 $\mu E/m^2/s$) is required for maximum photosynthesis of *S. robustus* indoors, and plants cannot be made to show saturation of CO_2 uptake by light (Pearcy et al. 1982). Elevated CO_2 concentrations increase the growth, photosynthesis, and water-use efficiency of *S. maritimus* (Rozema et al. 1991).

When growing in nutrient-poor sediments, *S. maritimus* concentrates nutrients in its aerial parts to a greater extent than several other common emergents (Dykyjova 1978). Plants cultured from corms and fertilized with ammonium sulfate increase rapidly in dry weight while taking up very little nitrogen (Visperas and Vergara 1976a). Clevering and Van der Putten (1995) grew *S. maritimus* seedlings indoors in experiments to determine whether large accumulations of detritus limit nutrient supplies and thus account for the poor growth of this bulrush in wetlands formerly influenced by tides but now impounded. They concluded that a combination of toxic organic compounds and anaerobiosis in roots was a more likely explanation. This species probably does not use nitrogen, phosphorus, or carbon from its belowground parts during the growing season (Hall and Yesaki 1988). Kaushik (1963) cultured *S. maritimus* from Utah in water with added calcium chloride and sodium chloride (1:2 ratio) and nutrients. At salinities greater than about 7.7 g/L, the plants accumulated less sodium, calcium, chloride, and magnesium but more potassium than the similarly treated freshwater species *Typha latifolia* and *S. acutus*. Only minimal increases in sodium and chloride occur in Phillipine *S. maritimus* shoots when potting soils contain more than about 0.8% sodium chloride (Mercado et al. 1971). When increasing amounts of potassium, nitrogen, phosphorus, and calcium are added to hydroponic culture solutions supporting growth of the freshwater subspecies (*S. maritimus* ssp. *maritimus)* from Czechoslovakia, the plants show little or no increased uptake of these ions (Dykyjova 1986). Dykyjova (1986) could not complete a similar nutrient-uptake experiment on the brackish water subspecies (*S. maritimus* ssp. *compactus*). Nevertheless, the seemingly increased ability of *S. maritimus* to control uptake of some of these ions probably is related to osmoregulation. High levels of magnesium, or lower levels in the absence of calcium, cause abnormal seedling development in Louisiana populations of *S. robustus*, but such conditions usually are not found in wetlands in that area and are probably not important in establishing stands of this species (Palmisano 1970). *Scirpus robustus* may have a relatively low ability to take up zinc, cadmium, nickel, lead, and chromium; all these metals as well as phosphorus and iron are found at higher concentrations in the roots than in the tops or rhizomes (Lee et al. 1976). Meiorin (1989) found highest concentrations of magnesium in leaves of *S. robustus*, whereas zinc was greatest in roots.

In summary, physiological and anatomical evidence indicates that *S. maritimus* and *S. robustus* are adapted to thrive in moderately saline, well-lit environments that experience high summer temperatures. Nutrient use patterns seem efficient. A selective uptake of sodium and chlorine ions and the manufacture of soluble carbohydrates may aid osmoregulation. The latter ability may also enhance survival in anoxic sediments.

Growth and Production

Except where specific references are given, the information in this section is from sources in Table 2.

Table 2. References and subject material about the growth, production, and chemical and caloric content of *Scirpus maritimus* and *S. robustus*.

Reference	Subjects examined
Christensen 1938	Nutrient and mineral content
Olsen 1945	Shoot density
Christensen et al. 1947	Nutrient content
Spinner and Bishop 1950	Achene nutrient content
Singleton 1951	Achene production
Neely 1960	Achene production
Jemison and Chabreck 1962	Achene production
Kaushik 1963	Chemical content
Bardwell et al. 1965	Achene nutrient content
Ungar 1965, 1968	Effects of salinity on density
Palmisano 1967	Production, reproduction, phenology
Waits 1967	Density, primary production, calorific content
Mall 1969	Achene production
Ungar et al. 1969	Effects of salinity on density
Burgess 1970	Achene production
Palmisano 1970	Mineral content
Dykyjova 1971	Biomass allocation
Mercado et al. 1971	Corm production, mineral content
Palmisano 1972	Effects of salinity on growth
Dykyjova 1973	Growth rate, biomass allocation
Ondok 1973	Shoot density
Cruz and Poe 1975	Nutrient content
Dykyjova and Pribil 1975	Chemical and calorific content
Yamanaka 1975	Chemical content
Visperas and Vergara 1976a	Growth rate, biomass allocation
Ondok and Kvet 1978	Shoot density
Prevost et al. 1978	Achene production
Barker and Fulton 1979	Shoot density, growth
Dykyjova 1978, 1979	Nutrient and mineral content
Fredrickson 1980	Nutrient content
Linthurst and Seneca 1980	Density, biomass allocation
Popp and Albert 1980	Amino acid content
Congdon and McComb 1981	Biomass allocation
Hanley 1981	Shoot density
Lieffers and Shay 1981	Effects of water levels on production
Podlejski 1981, 1982	Density, productivity
Barclay and Crawford 1982	Shoot growth under anaerobiosis
Briens and Larher 1982	Water and ash content
Duncan and D'Herbes 1982	Density, effects of grazing
Lieffers and Shay 1982a	Effects of water depth and salinity on production
Lieffers and Shay 1982b	Effects of environmental variables on growth
Pearcy et al. 1982	Effects of salinity on production, nutrient content
Smith and Kadlec 1983	Density
Euliss 1984	Achene production
Krisch 1985	Biomass, shoot density, water content
Bernasor and De Datta 1986	Shoot density
Dykyjova 1986	Production ecology, chemical content
Krisch 1986	Density
Hall and Yesaki 1986	Density, nutrient content
Schuler 1987	Achene production
Pehrsson 1988	Achene production, shoot density
Kikuchi et al. 1989	Density, biomass, nutrient content
Hothem and Ohlendorf 1989	Achene selenium and water content
Meiorin 1989	Mineral content
Karagatzides and Hutchinson 1991	Biomass, density
Clevering and Van der Putten 1995	Effects of detritus on seedling growth

Rate

Scirpus maritimus cultured indoors from mature corms in fertilized soil grows in three phases. During the first 20 days after planting, only shoots grow and the dry weight of plants increases slowly. During the next 100 days, dry matter increases rapidly, the rhizome network expands, shoot numbers peak, and leaf areas reach the maximum size. Single corms can produce as many as 83 shoots, mostly from the rhizomes, in 100 days. Rapid increases in shoot growth precede rapid increases in corm weight. During the next 90 days, the growth rates of shoots, rhizomes, and roots decline, leaves senesce and shoots die, but corm weights increase and ultimately account for most dry matter. Plants can grow as fast as 2.7 cm/day during the first 40 days and reach maximum height in 80 days. Even when crowded, a single corm can produce 4.5 m of corm-bearing rhizomes in 40 days. Plants grown from mature corms planted in outdoor ponds can emerge from 90 cm deep water after 9 weeks of submerged growth.

Density and Yield

Stem or shoot density in healthy stands of *Scirpus maritimus* and *S. robustus* is usually about 50-500/m^2 (max. 564/m^2 in *S. maritimus;* Krisch 1985). During periods of peak biomass, plants seldom shade more than 30-50% of the water or bottom surface.

During dormant periods, nearly 100% of the total live biomass of both bulrushes is below ground. In mature stands, total belowground net production can be as much as three times that of aboveground production, and belowground biomass at times of maximum biomass can be six times aboveground biomass. Peak live standing crop biomass is usually only slightly higher than annual net primary production. Dry aboveground biomass or net annual primary production in healthy stands often exceeds 500 g/m^2 but seldom exceeds 1,500 g/m^2 (Table 3). Much greater biomasses are obtained in culture (Dykyjova 1978).

Annual yields of *S. robustus* achenes sometimes reach 567 g/m^2 fresh weight, but production in most stands managed for wintering ducks is usually less than 150 g/m^2. Amounts available for consumption in any given month are usually less than 50 g/m^2. Achene production in managed stands of *S. maritimus* is usually less than 100 g/m^2. A single *S. maritimus* plant in indoor culture may produce as many as 366 corms and a single corm as many as 28.7 shoots (Mercado et al. 1971).

Distribution of biomass and growth characteristics of *S. maritimus* strongly relate to habitat. Stands where sediments accumulate or where water depths decrease during the growing season have many leaves and shoots near the water or sediment surface, and plants usually produce copious flowers and fruits. Biomass concentrates in photosynthetic tissue and stems when water depths are low. In contrast, plants growing in erosional biotopes or where water depths increase during the growing season often lose their young leaves. Shoots unable to reach the water surface die. Biomass concentrates in reproductive panicles on the few stems that reach the water surface. In later sections, I address other biotic or abiotic factors that affect or limit biomass.

Chemical and Caloric Content

Water content of the aboveground parts of *Scirpus maritimus* averages about 79% during the reproductive period. The water content of *S. maritimus* leaves is about 75% of fresh weight, much less than the 87.5% found in the roots. The moisture content of the achenes averages about 31.1%. On an air-dried basis, the water content of *S. maritimus* is: stems and leaves 6.6-9.4%, achenes 8.6-12.8%, and corms 13.6%. Air-dried *S. robustus* achenes contain about 7.7% water.

The ash content of whole *S. maritimus* plants is about 6.2-14.0% of dry weight. The leaves have the most ash (13.0-15.1%); stems (11.2%), roots (6.0%), corms (4.4-6.4%), and achenes (2.2-5.4%) have less. The achenes of *S. robustus* have 3.2-6.4% ash.

The maximum gross energy of dry aboveground parts of *S. robustus* is about 4.5 kcal/g. Energy in *S. maritimus* is similar (3.8-4.3 kcal/g). Energy in dry *S. maritimus* corms averages 4.8 kcal/g and in achenes 4.1 kcal/g. Apparent metabolizable energy (AME) of *S. maritimus* or *S. robustus* achenes is about 3.2 kcal/g (Miller 1987).

The crude protein in achenes and total aboveground parts of both species likely does not exceed 9.1% of the dry weight. The average protein content is much higher in leaves and stems (10-11% of dry weight) of *S. maritimus* than in flowering panicles (6-7% of dry weight). In oven-dried (103° C) parts of *S. robustus*, crude protein is 5.7% in shoots and 5.5% in belowground parts. I found no other information on crude protein content of this species. Popp and Albert (1980) and Cruz and Poe (1975) listed the principal amino acids in both species.

Crude fat content in the achenes of both species is about 2.3-4.3% of dry weight. In *S. maritimus*, crude fat content is greater in the total aboveground parts (2.2-2.4% of dry weight) than in the corms (0.8%). I

Table 3. *Scirpus maritimus (S.m.)* and *S. robustus (S.r.)* peak aboveground biomass or standing crop (AG) or annual net primary production (NPP), belowground biomass (BG) or annual net belowground production (BNP), and probable factors limiting biomass.

		Biomass[a]		
Reference	**Species**	**AG or NPP**	**BG or BNP**	**Probable limiting factors**
Schuler 1987	*S.m.*	0.4		competition by other helophytes
Chandler 1969	*S.r.*	15		competition by other helophytes
Waits 1967	*S.r.*	19		competition by other helophytes
Lieffers and Shay 1982a	*S.m.*	27		drought, increased salinity
Handoo and Kaul 1982	*S.m.*	71		competition by other helophytes
Kaul et al. 1978	*S.m.*	59	42	competition by other helophytes
Linthurst and Seneca 1980	*S.r.*	67		drought, increased salinity
Smith and Odum 1981	*S.r.*		87	grazing by geese
Grillas and Duncan 1986	*S.m.*	89		livestock grazing, excessive water depth
Foote et al. 1988	*S.m.*	109		insect herbivory
Kikuchi et al. 1989	*S.m*	117	54	mineral-poor substrate
Ondok 1971	*S.m.*	137		none indicated
Komarkova 1973	*S.m.*	167		high water levels
Ondok 1973	*S.m.*	167		none indicated
Foote et al. 1988	*S.m.*	202		none indicated
Kikuchi et al. 1989	*S.m.*	205	43	none indicated
Smith and Odum 1981	*S.r.*		220	none indicated
Waits 1967	*S.r.*	270		none indicated
Shubert 1982	*S.m*	280		none indicated
Podlejski 1982	*S.m.*	291	1,320	cattle grazing
Linthurst and Seneca 1980	*S.r.*	292		none indicated
Glooschenko 1978	*S.m.*	308		none indicated
Komarkova and Marvan 1978	*S.m.*	334		none indicated
Dykyjova and Pribil 1975	*S.m.*	378		erosion of bottom substrate
Krisch 1985	*S.m.*	380		competition by other helophytes
Bernasor and De Datta 1986	*S.m.*	385		competition by rice (*Oryza sativa*)
Krisch 1985	*S.m.*	395		competition by other helophytes
Podlejski 1981	*S.m.*	415	665	reduced fertility of bottom substrate
Yamanaka 1975	*S.m.*	462		none indicated
Ewing 1986	*S.m.*	480		competition by other helophytes
Ondok and Dykyjova 1973	*S.m.*	480		none indicated
Dykyjova 1986	*S.m.*	544		erosion of bottom substrate
Kibby et al. 1980	*S.m.*	550		none indicated
Olson 1979	*S.m.*	551		none indicated
Mall 1969	*S.r.*	552		competition by other helophytes
Lieffers and Shay 1982a	*S.m.*	625		none indicated
Moody 1978	*S.m.*	627		none indicated
Dykyjova 1986	*S.m.*	678	373	none indicated
Fiala and Kvet 1971	*S.m.*	680	1,107	none indicated
Smith and Kadlec 1985c	*S.m.*	722		grazing by waterfowl and muskrats
Pearcy et al. 1982	*S.r.*	800		none indicated
Kvet 1978	*S.m.*	820		none indicated
Smith and Kadlec 1985c	*S.m.*	849		none indicated
Hall and Yesaki 1988	*S.m.*	862	342	none indicated
Dykyjova and Pribil 1975	*S.m.*	866		none indicated
Dykyjova et al. 1971	*S.m.*	908		none indicated
Krisch 1986	*S.m.*	922		none indicated
Lieffers and Shay 1982b	*S.m.*	936	738	none indicated
Krisch 1985	*S.m.*	958		none indicated
Palmisano 1967	*S.r.*	961		none indicated
Dykyjova 1986	*S.m.*	998		none indicated
Podlejski 1982	*S.m.*	999	2,348	none indicated
Karagatzides and Hutchinson 1991	*S.m.*	<1,000	<3,000	excessive tidal inundation
Karagatzides and Hutchinson 1991	*S.m.*	>1,000	>3,000	none indicated
Congdon and McComb 1981	*S.m.*	1,100	1,000	none indicated
Podlejski 1981	*S.m.*	1,061	2,070	none indicated
Eilers 1975	*S.m.*	1,164		none indicated
Kvet and Husak 1978	*S.m.*	1,300	2,800	none indicated

[a] Biomasses in g/m^2 dry weight. Belowground biomasses measured at time of peak aboveground biomass. Dry weight = 0.25 (fresh weight) = 1.14 (ash-free dry weight).

found no information on the fat content of other parts of *S. robustus*.

Whole *S. maritimus* plants contain about 42-47% carbohydrates on a dry-weight basis. Carbohydrates are higher in the flower heads than in the stems or leaves. Carbohydrate reserves in *S. robustus* corms can attain 86% of dry corm weight. I found no similar information about *S. maritimus* corms. Carbohydrates in *S. maritimus* and *S. robustus* achenes compose about 59% and 67% of dry weight. The principal sugars in *S. maritimus* rhizomes are known (Barclay and Crawford 1983).

Fiber content in the achenes in *S. maritimus* is lower (15-25% of dry weight) than in the stems and leaves (21-33% of dry weight). *Scirpus robustus* achenes are about 14-16% dry weight fiber. Crude fiber content of *S. maritimus* corms is about 10% of dry weight; no information is available about *S. robustus* corms. Lignin content of aboveground parts of *S. maritimus* averages 10.3-11.6% of the dry weight and 12.1-12.8% of the ash-free dry weight.

I list other elements and compounds in various parts of *S. maritimus* and *S. robustus* (Table 4). The ability to take up nutrients in nutrient-rich environments is lower by *Scirpus maritimus* than by representatives of other common emergent genera such as *Phragmites, Glyceria, Sparganium,* and *Typha* (Dykyjova 1986). Hothem and Ohlendorf (1989) report selenium concentrations as high as 8.8 μg/g of dry weight in *S. maritimus* achenes from a California reservoir. Little is known about concentrations of other potentially toxic elements in either bulrush species (Outridge and Noller 1991).

In summary, *S. robustus* (and probably *S. maritimus*) corms have high carbohydrate concentrations. Achenes are also high in carbohydrates and crude fat. Both bulrushes probably are inelastic in their ability to take up nutrients and are thus probably poor candidates for use in removing nutrients from industrial or domestic effluents.

Decomposition

Decomposition of *Scirpus maritimus* begins in September in tidal Oregon wetlands; aboveground parts slowly disappear throughout the winter, and by spring only a few withered stems, 7.5-15 cm tall, remain attached to the cormous roots (Eilers 1975). Hall and Yesaki (1988) noted that mortality of *S. maritimus* peaks in September or October in a British Columbia estuary when dead material increases 6.3 g AFDW (ash-free dry weight)/m^2/day. They found that about 85% of the total standing crop enters the detritus pool, and 74% of this dissipates to the estuary and 26% becomes buried in sediments. In Saskatchewan, stems begin dying after September frosts but generally remain standing over winter (Lieffers and Shay 1982*a*). In the Camargue of France, dead stems of *S. maritimus* first appear in July and August when early drying probably promotes senescence (Podlejski 1982). Because *S. maritimus* develops a central woody core by the end of the growing season (Moody 1978) and lacks the buoyancy and larger stem size of some of the other bulrushes, many plants sink and are covered by sediment (Hall and Yesaki 1988). Nevertheless, plant parts washed ashore by tides and decomposed are sometimes an important source of sediment nitrogen for other plants (Beeftink 1966). In small wetlands reclaimed from the sea, where wave action is not severe, *S. maritimus* detritus accumulates in the centers of circular stands (Clevering and Van der Putten 1995).

Scirpus robustus stems stay erect all winter (Neely 1960). Unlike most other salt marsh emergents in North Carolina, *S. robustus* plants in experimental decomposition bags lose weight slowly (Waits 1967). Achenes lose only 3% of their original weights after submergence for 30 days (Shearer et al. 1969). A similar experiment by Neely (1956) showed that *S. robustus* achenes lose only 1% of their original weights after 90 days, a slower rate than that of seeds of 24 other plants eaten by ducks.

Habitat and Associated Abiotic Limiting Factors

Coastal Wetland Types

The principal natural habitat of *Scirpus maritimus* and *S. robustus* is estuarine intertidal emergent wetland as classified by Cowardin et al. (1979). Communities where *S. maritimus* is dominant or relatively important usually are between 1.8 m below the mean low low water (MLLW) and 2.6 m above MLLW (Jefferson 1974; Eilers 1975; Riley and McKay 1980; Frenkel and Boss 1988). In the Pacific Northwest, Karagatzides and Hutchinson (1991) found much larger peak standing crops in the higher parts of the intertidal zone than in the low parts that are submerged for longer periods. In the Puget Trough, communities dominated by *S. maritimus* are a distinguishing feature of the fluvially influenced portions of coastal wetlands (Hutchinson 1988). These communities also occur in saline areas in unconsolidated, anoxic muck (Ewing 1983). Ewing and Kershaw (1986) noted the most well-developed stands of *S. maritimus* around the mean high water (MHW) mark on James Bay, where

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Table 4. Chemical composition of various parts of *Scirpus maritimus* and *S. robustus* from wild populations.

Species/ Plant parts analyzed	Unit of measurement[a]	N	NH_3	P	K	C	Na	Ca	Mg	Cl	Na_2O	K_2O	CaO	P_2O_5	MgO	Reference[b]
S. maritimus																
whole aboveground	% d.w.	1.34		0.16				0.76	0.58							1
whole aboveground	% d.w.	0.84-0.94														2
stems and leaves	% d.w.	0.78														3
stems	% d.w.	1.29-1.35		0.16-0.20				0.31-0.52	0.99-1.10							4
shoots at maximum biomass	% d.w.	1.36-1.79		0.28-0.35	1.40-2.69		0.08-0.63	0.16-0.66	0.10-0.17							5
shoots at maximum biomass	% d.w.	1.36-1.89		0.27-0.31	1.40-1.84		0.15-0.66	0.12-0.63	0.13-0.17							6
shoots throughout season	% d.w.	1.36-3.15		0.27-0.52	1.40-3.28		0.66-1.15	0.08-0.63	0.05-0.17							6
live parts	% AFDW					45.3-47.9										7
young shoots	% AFDW	3.15		0.41												7
corms of current season	% d.w.	0.94-2.45		0.31-0.52	0.96-1.72		0.11	0.03	0.06-0.10							6
corms of previous season	% d.w.	1.17-1.68		0.40	0.56-1.07		0.13	0.02-0.19	0.06-0.11							6
corms	% d.w.	0.84														3
corms	% d.w.	1.19		0.29				0.36	0.16							4
achenes	% d.w.	2.4-3.1														3
achenes	% ash									0.56	1.95	0.40	30.2	0.94	6.45	8
roots and rhizomes	% AFDW	1.6		0.21												7
roots and rhizomes	% d.w.	0.79		0.19				0.43	0.35							4
roots	% d.w.	0.92		0.45				0.48	0.37							4
rhizomes	% d.w.	0.84		0.21				0.12	0.39							4
S. robustus																
shoots	mg/g d.w.		2.6													9
roots	mg/g d.w.		1.6													9
achenes	% d.w.			0.22				0.06								10

[a] d.w.=dry weight; AFDW=ash-free dry weight

[b] References: (1) Christensen et al. 1947;(2) Yamanaka 1975; (3) Fredrickson 1980; (4) Kikuchi et al. 1969; (5) Dykyjova 1973; (6) Dykyjova 1986; (7) Hall and Yesaki 1988; (8) Christensen 1938; (9) Cruz and Poe 1975; (10) Bardwell et al. 1965.

salinities are higher than in the lower marsh. Stands there are restricted to narrow areas on recently prograded (exposed by a rebounding land surface) backshores where upward groundwater flows create brackish conditions (Price et al. 1988). Along the Dutch coast, *S. maritimus* grows in reed swamps, dune slacks, and higher-elevation salt marshes (Haeck et al. 1985). Where tidal fluctuations are small, such as in southeastern Norway, stands usually occur from about 75 cm above to just below mean sea level (MSL; Vevle 1985).

Water regimes of wetlands that support *S. maritimus* are variously described as irregularly exposed; irregularly, temporarily, seasonally, and permanently flooded; and saturated (Bassett 1978; Britton and Podlejski 1981; Ferren 1985; Grillas and Duncan 1986). In tidal Oregon wetlands, monotypic stands of *S. maritimus* occur in areas continuously submerged for a maximum of 6-9 h/24-h period annually. These stands are never continuously exposed for a full day (Eilers 1975). Similarly, stands in British Columbia estuaries occur where sediments are always saturated (Kennedy 1982). In France, populations occur in coastal wetlands that usually dry up in July or August and refill in October or December; the most well-developed stands grow at sites protected from strong wave action (Podlejski 1981). Stands in Spain occur on the banks of saline lagoons flooded more than 3 months/year (Garcia et al. 1993). Haslam (1987) associated this species with turbid and semiturbid waters where macrophytes are not visible more than 75 cm below the water surface.

Habitats of coastal populations of *S. robustus* are similar. Along the South Atlantic and gulf coasts, the best habitat is irregularly flooded salt marshes whose bottoms are covered by wind tides at irregular intervals (Uhler and Hotchkiss 1968). In North Carolina, this bulrush is most common in the transitional area between the lower zones of the irregularly flooded marsh and the upper zones of the regularly flooded marsh as well as in openings in the irregularly flooded high marsh that flood several times a month (Waits 1967; Heitzman 1978). These areas flood to very shallow depths, but water recedes slowly. *Scirpus robustus* stands occur at mean elevations of about 60 cm above MSL in North Carolina (Waits 1967) and 67-84 cm above MSL in Delaware (Bourn and Cottam 1950). Linthurst and Seneca (1980) found stands at elevations near 13 cm above MHW in North Carolina, whereas most plants occur near 40 cm below MHW in the nearby Chesapeake Bay (Flowers 1973). In Louisiana, Sasser (1977) found this bulrush mostly in areas at or slightly below mean water level. There, and in California, *S. robustus* is mostly found in the brackish marshes between saline and fresh marshes (Palmisano and Newsom 1968; Atwater and Hedel 1976). However, some Louisiana populations border the Gulf of Mexico or occur more than 80 km inland (Palmisano 1970; Brewer and Grace 1990).

Interior Wetland Types

Populations of *S. maritimus* in the interior grasslands of central North America mostly occur in palustrine mixosaline wetlands (Cowardin et al. 1979) or in semipermanent brackish and subsaline wetlands (Fig. 2; Stewart and Kantrud 1971). These wetlands tend to be shallower and contain surface water for shorter periods than semipermanent fresh or slightly brackish wetlands (Millar 1976). In North Dakota, Metcalf (1931) differentiated between saline lakes dominated by *S. maritimus* and other saline lakes that dried out earlier or later and had less emergent vegetation. Plants sometimes occur in seasonally flooded basins but may disappear with higher water levels (Millar 1973). *Scirpus maritimus* also occurs in lacustrine wetlands (Ungar 1965, 1968, 1970; Stewart and Kantrud 1971; Lieffers and Shay 1982b) and in oxbows (Lieffers 1984). In the Great Basin, plants expand slowly into continually flooded areas but quickly colonize barren salt flats when shallow water flows are maintained for 2-3 years (Nelson 1954; Kadlec 1982). Inland populations also occur worldwide in a wide variety of natural and impounded wetlands (Dykyjova 1986) and in rice fields (Bassett 1978; Podlejski 1981, 1982; Ferren 1985; Bernasor and DeDatta 1986). *Scirpus maritimus* and putative *S. glaucus* × *maritimus* hybrids also grow in rice fields in California (Browning et al. 1995; see the taxonomy and distribution section).

In summary, both bulrushes characterize estuarine wetlands at elevations near mean sea level where wave action is not severe. Stands also occur in slightly higher areas where groundwater-derived salts accumulate. In the continental interiors, *S. maritimus* occurs in palustrine wetlands with a wide variety of water regimes. Both species flourish in impoundments and rice fields.

Water Column

Depth

Scirpus maritimus and *S. robustus* are species of relatively shallow (less than 1 m deep) waters (Table 5). *Scirpus robustus* may be less tolerant of deep water, although few records are available. *Scirpus*

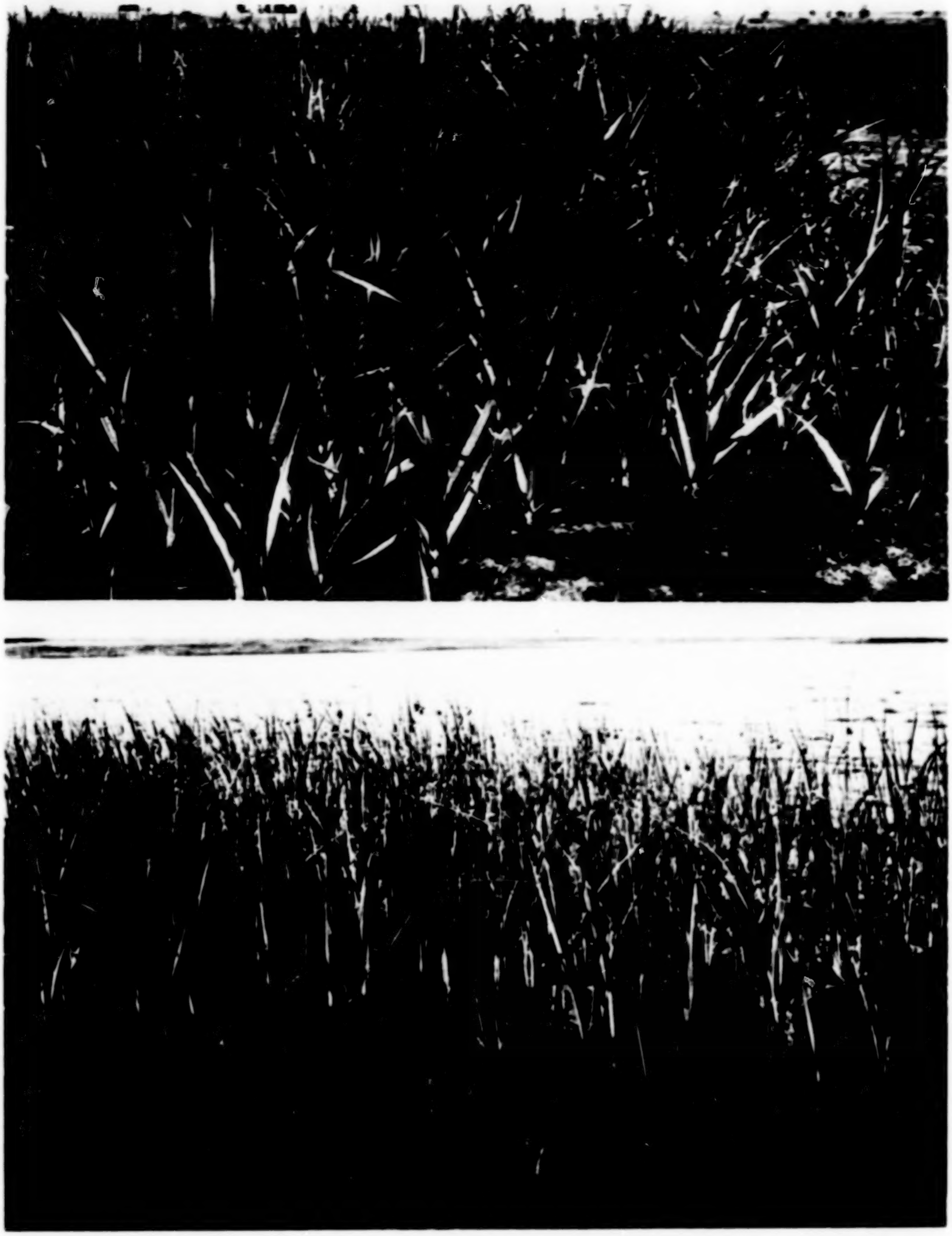

Fig 2. Natural stands of *Scirpus maritimus* in the same mesosaline, semipermanently flooded wetland in North Dakota. Upper photograph, taken 3 August 1961 where surface water had been absent for about 1 month, shows short plants with large numbers of robust inflorescences. Lower photograph, taken 3 August 1962 where surface water had been present throughout the growing season, shows taller plants with fewer, smaller inflorescences. Photographs by R. E. Stewart.

Table 5. General habitat features for *Scirpus maritimus* and *S. robustus* arranged according to increasing observed tolerance of water depth.

Depth (cm)[a]				
Range or single observation	Optimum[b]	Predominant water salinity[c]	Predominant sediment texture	Reference
Scirpus maritimus				
5-10				Ondok 1971
>10				Vince and Snow 1984
5-22		mixosaline	decomposed peats	Richardson 1980
0-25			various	Nelson 1954
tr.-29	tr.	mixosaline	silt	Olson 1979
16-30				Smith, L. 1983
33				White and Hartland-Rowe 1969
2-40		mixosaline		Van Donselarr et al. 1961
10-50			sand	Krisch 1985
24-59	30-59	mixosaline	silt	Grillas and Duncan 1986
0-65	25-35	mixosaline, eusaline	clay to sand	Lieffers and Shay 1982b
20-70	20-50	mixosaline	gyttja, clay	Lundegardh-Ericson 1972
0-70	18-35	mixosaline		Podlejski 1981
70-80				Ondok 1973
0-90	20-80	fresh		Fiala and Kvet 1971
40-90			sand	Dykyjova 1973
Scirpus robustus				
tr.-4				Waits 1967
0-13		mixosaline		Chandler 1969
0-13		mixosaline		Palmisano and Newsom 1968
0-20		mixosaline		Palmisano 1970
3-30	10-23			Mall 1969
0-47		mixosaline		Soileau 1968

[a] tr. = .05 cm; minimum depths given as 0 where depths to groundwater (negative depths) were given.

[b] Optimum depths as stated by author, where maximum aboveground biomass or frequency was shown in tables or graphs, or where best propagation results were obtained.

[c] Water chemistry classes of Cowardin et al. (1979).

maritimus seems to tolerate greater depths in freshwater or where bottoms are sandy, but these may be attributes of European subspecies (Dykyjova 1986).

Lieffers and Shay (1982b) measured 27 environmental variables in 24 Saskatchewan wetlands ranging from mixosaline to eusaline classified according to Cowardin et al. (1979). Of all the variables, mean water level correlated most with growth measures of *S. maritimus*. However, Lieffers and Shay (1982b) found that salinities vary colinearly with mean water levels. For example, during a year when the mean water level was 9 cm below the sediment surface in a stand of *S. maritimus*, the mean water conductivity was 55 mmho/cm and plant biomass was 21 g/m^2 dry weight. During another year, water depth was 16 cm above the sediment surface, conductivity fell to 12.3 mmho/cm, and *S. maritimus* biomass was 386 g/m^2 dry weight. Lieffers and Shay (1982b) also found that in all wetlands, stem densities peak at depths of about 25 cm, but aboveground biomass is highest when depths average 35 cm. This species withstands at least 5 years of dryness (Chapman 1974).

Clonal growth replaces seed production when water levels are high (Lieffers and Shay 1981). *Scirpus maritimus* plants in 40-cm-deep water may be only 5 cm taller but have nearly three times as many shoots and much greater leaf area than plants in water more than twice as deep (Dykyjova 1973). Belowground growth also decreases in deeper, fresher water (Dykyjova et al. 1972). Fiala and Kvet (1971) show how depth distribution of *S. maritimus* varies with exposure and probable competition: plants in exposed sites, where *Typha* and *Phragmites* are absent, grow in broad zones at depths from about 20 to 90 cm, but in sheltered locations where the two competitors dominate deeper waters, plants are restricted to narrow bands at about 40 cm depth.

In tidal wetlands in the Netherlands, the depth range of *S. maritimus* varies with tidal exposure (Coops and Smit 1991). Plants subjected to full tidal influence are found where water depth varies from just below to more than 1 m above MHW, whereas plants in areas with smaller tides shift toward the low waterline. The range of occurrence is smaller in wetlands that are totally separated from the sea than in tidally influenced areas. Coops and Smit (1991) found no overall relation between water depth and stem density, flowering percentage, or floral culm length at any sites but noted seedling production only in the tidally influenced areas. But when they held water at various depths above planted corms in outdoor containers, the numbers of leaves peaked at depths of 0-30 cm, belowground and aboveground biomass and culm width were greatest at depths of 30 cm, new shoot formation and flowering percentage were greatest at depths of 30-60 cm, and culm length was greatest at depths of 60 cm.

Temperature

The widespread distribution of *S. maritimus* suggests that this species tolerates a wide range of water temperature. In an Alberta lake inhabited by *S. maritimus*, water temperatures from April to August range from 0 to 32° C and closely follow air temperatures because the lake is shallow and turbid (White and Hartland-Rowe 1969). Van Wijk (1988) recorded water temperatures of 13.5-28.0° C during the growing season in a European wetland supporting *S. maritimus*. In Maryland, *S. robustus* grows where annual water temperatures range from -0.8 to 31° C; spring and summer water temperatures average 11.9° C and 25.6° C, respectively (Dietert and Shontz 1978).

Chemistry

Water salinity is a major factor in the distribution of *S. maritimus* and *S. robustus* in coastal and interior wetlands (Beeftink 1966; Stewart and Kantrud 1972; Hutchinson 1982; Newling et al. 1983; Lewis 1990; Shisler 1990). *Scirpus maritimus* occurs in waters containing 0.162-308 g/L salts, whereas *S. robustus* does not occur where salinities exceed 30 g/L (Table 6).

In most coastal areas, stands of *S. maritimus* usually develop best in the mesohaline portions of estuaries where freshwater flows into areas periodically immersed in seawater or the transitional areas between the sea and adjacent freshwater wetlands (Purer 1942; Filice 1954; Klavestad 1957; Beeftink 1966; Martini et al. 1979). The most well-developed stands are near the mouths of estuaries receiving substantial inflows of freshwater because salinities there are reduced (Ranwell 1972). However, *S. maritimus* may be absent from coastal wetlands where seawater salinity is low, such as on the northern Baltic (Siira 1970). In British Columbia, this species invades habitats when growing-season salinities of interstitial water fall to 3.5-15.5 g/L during early summer because of inflows of fresh river water (Hutchinson 1982).

Obligate halophytes in full-strength seawater must develop cell-sap osmotic pressures greater than 20 bars to survive (Ranwell 1972). Arnold (1955, cited in Ranwell 1972) showed that the osmotic pressure of *S. maritimus* is only 14.9 bars, and therefore Ranwell considered the plant a facultative halophyte that also persists in nonsaline habitats. Dodd and Coupland (1966a) found similar low pressures in this species. Lohammar (1965) considered the plant a freshwater species in some parts of Sweden. Although plants may be less abundant, the fresher parts of an estuary can support stands of *S. maritimus* that are more robust and stay greener longer than in the more saline parts (Gillham 1957).

Inland populations of *S. maritimus* thrive in mesosaline (Cowardin et al. 1979) waters, where salinities usually are about 8-30 g/L (Metcalf 1931; Stewart and Kantrud 1972). However, stands occur in polysaline, eusaline, and even hypersaline waters where salinities sometimes exceed 300 g/L (Hammer and Heseltine 1988). During periods of low water, when evaporation raises salinities from a few grams per liter to around 10 g/L, *S. maritimus* frequently occurs in prairie wetlands normally dominated by *Typha* spp. and *S. acutus* (Krapu and Duebbert 1974; personal observation). Husak and Hejny (1978) also noted that in relatively fresh Czechoslovakian wetlands, *S. maritimus* communities become well established only in years when water levels are low. Millar (1969) opined that *S. maritimus* requires high salinity to survive in prairie wetlands, but because experiments show that the species flourishes in freshwater, he attributed its survival to the intolerance of other plants to saline environments. Nevertheless, the scarcity of *S. maritimus* in fresher prairie wetlands suggests an inability to compete with glycophytes there (Ungar 1974; Hammer and Heseltine 1988).

Scirpus robustus, which seldom occurs far from coastal waters, is a freshwater plant, according to Hackney and Cruz (1982). Others consider the plant a member of the oligohaline (0.5-5.0 g/L) or polyhaline (18-30 g/L) plant communities (Lewis 1990; Shisler 1990). Its optimum habitat seems to be wetlands with water salinities of about 3-10 g/L (Table 5).

Table 6. Salinities of waters inhabited by *Scirpus maritimus* and *S. robustus* arranged according to increasing maximum observed salt tolerance.

Salinity or total dissolved solids (g/L)[a]			
Range or single observation	Optimum	Dominant anions[b]	Reference
Scirpus maritimus			
0.304		HCO_3	Kaul et al. 1978
>1.26			Willen 1962
0.98-1.33			Fulton et al. 1983
0.454-1.481		SO_4	Gladyshev and Kogan 1977
2.333			Barker and Fulton 1979
2.83		SO_4	Eisenlohr 1972
<3.8		SO_4/CO_3	White and Hartland-Rowe 1969
4.3-4.5		Cl	Lundegardh-Ericson 1972
<5.0		Cl	Flowers 1973
4.45-5.34		Cl	Mercado et al. 1971
0.18-5.96		Cl	Van Wijk 1988
<7.0		Cl	Barnes et al. 1971
	7.667	SO_4	Olson 1979
<8.0		SO_4	Daborn 1975
8.0		Cl	Vestergaard 1985
8.2			Lieffers 1984
9.0			Shubert 1982
2.56-9.08			Smeins 1967
3.9-9.3		Cl	Grillas and Duncan 1986
3.2-9.6		Cl	Ferren 1985
10.0		Cl	Harshberger 1911
1.5-13.5		Cl	Kruger and Kirst 1991
7.5-14.0		Cl	Olsen 1945
2.6-14.2			Kadlec 1982
<16.0	1.6-6.4	Cl	Gillham 1957
<19.6			Christiansen and Low 1970
3.0-20.0		Cl	Zenkevitch 1963
<21.684		Cl	Podlejski 1981
4.3-23.5		Cl	Verhoeven and van Vierssen 1978
2.4-25.9		Cl	Wright et al. 1949
<31.95		Cl	Tansley 1922
0.162-37.002			Sletten and Larson 1984
7.0-50.0			Ustin 1984
5.0-55.0			Richardson 1980
<67.5			Millar 1976
1.61-78.00		SO_4	Lieffers and Shay 1982a
1.88-82.40	1.88-30.27		Metcalf 1931
0.56-87.00		SO_4	Leiffers and Shay 1982b
7.0-104.0			Unger 1970
0.56-114.60			Kantrud et al. 1989
3.3-121.0		SO_4	Hammer et al. 1975
3.2-308.0		SO_4	Hammer and Heseltine 1988
Scirpus robustus			
0.2-3.6		Cl	Philipp and Brown 1965
3.02-6.31		Cl	Beal 1977
8.9			Chabreck 1972
1.380-9.217		Cl	Chandler 1989
4.1-9.4		Cl	Kerwin 1971

Table 6. *Continued.*

Salinity or total dissolved solids (g/L)[a]			
Range or single observation	Optimum	Dominant anions[b]	Reference
3.195-9.585	3.834-9.585		Martin and Uhler 1939
1.0-10.0	3.0-7.0	Cl	Neely 1960
0.32-10.20		Cl	Waits 1967
9.5-10.2			Chabreck and Hoffpauir 1962
8.2-13.2		Cl	Anderson et al. 1968
0.9-18.2		Cl	Chabreck 1960
5.4-20.4		Cl	Dietert and Shontz 1978
12.0-21.6			Palmisano 1967
22.0			Taylor 1939
8.0-22.8		Cl	Wilkinson 1970
11.4-25.9		Cl	Wright et al. 1949
1.0-29.0	8.2	Cl	Chabreck 1970
13.0-29.0		Cl	Atwater and Hedel 1976
10.0-30.0		Cl	Linthurst and Seneca 1980
18.0-30.0		Cl	Shisler 1990
6.4-39.0			Penfound and Hathaway 1938

[a] Conductivity was converted to mg/L with the following multipliers: 0-2 mS/cm x 0.7; 2-40 mS/cm x 1.0; 40 mS/cm x 1.5. Chlorinity (0/00 or g/L) was converted to mg/L by multiplying by 1.807×10^3; sea strength was considered 31,950 mg/L. Total filtrable residue was considered equal to total dissolved solids.

[b] Where ranges are listed, dominant anions refer to those found at the upper range.

Scirpus robustus is less salt tolerant than most common salt marsh species. Stands develop best between uplands and intertidal marsh where there is some freshwater runoff (Johnson and Raup 1947; Bourn and Cottam 1950; Shellhammer et al. 1982; Newling et al. 1983; Zedler and Beare 1986). Impoundments may be the sources of these freshwaters (Whitman and Cole 1987). The occurrence of *S. robustus* in brackish to saline sites may involve ecological displacement rather than an optimum response to the environment (Pearcy et al. 1982). Plants sometimes occupy areas between stands of more salt-tolerant species (Ustin et al. 1982).

Palmisano (1970) used nutrient solutions and artificial seawater to show that only about 50% of *S. robustus* plants survive at salinities of 17 g/L; the upper limit of growth is about 21 g/L. His experiments with nutrient solutions and sodium chloride showed that growth is reduced 50% at 10 g/L and that growth almost ceases at 30 g/L. He also showed that culm growth is more restricted than root growth at higher salinity levels. The mean water salinity in natural stands in Palmisano's (1970) study area was 1.06 g/L.

Water salinity affects various aspects of the reproduction and growth of *S. maritimus* and *S. robustus*. Indoor greenhouse experiments of Kaushik (1963), who added calcium chloride and sodium chloride (1:2 ratio) and nutrients to tap water for his test solutions, showed that achene germination of *S. maritimus* decreases as salinities increase to about 15.4 g/L. At higher salinities, achenes probably cannot absorb enough water to germinate. Injury of achenes by salinity is in direct proportion to salt concentrations and length of treatment. With young plants, increased salinity reduces length, fresh weight, and number of leaves per plant as well as length of roots and root hairs. However, mortality (greater than about 20%) of young plants is not significant until salinities increase to about 5.8 g/L. In adult plants, stem diameter, height, and weight are reduced by salinities above this level. Kaushik (1963) also measured several reproductive variables and mortality of adult plants with the same test solutions. Unlike the growth measures, salinities of about 5.8 g/L stimulate spikelet and achene production. Mortality of adult *S. maritimus* begins when salinities reach about 11.5 g/L. Two-thirds of the plants die when salinities are raised to about 15.4 g/L for 8.3 days.

Corms also germinate best in freshwater (Mercado et al. 1971) but can withstand high salinities (Lieffers and Shay 1982b). Indoor tests by Mercado et al. (1971) revealed germination inhibition in *S. maritimus* corms held 9 days in a 23.4 g/L sodium chloride solution. However, 20% of the corms held for 9 days in solutions as saline as 29.2 g/L germinate after transfer to freshwater for 8 days. Mercado et al. (1971) also showed that plants grown in 4-10 g/L sodium chloride solutions produce larger numbers and weights of corms than plants grown in dilute solutions. *Scirpus maritimus* shows less belowground growth in deeper, fresher water (Dykyjova et al. 1972).

Dietert and Shontz (1978) found that 6-week-old cultured seedlings of *S. robustus* irrigated with freshwater grow much taller than those irrigated with 10 g/L salinity water and that 20 g/L water retards all growth. During this study, achenes were collected in an area where natural salinity was 11.4 g/L (spring) and 12.3 g/L (summer). Later culture experiments showed that even low levels of salinity inhibit growth of this species, whereas photosynthesis is inhibited only at moderate to high salinities (Pearcy and Ustin 1984). Salt tolerance of *S. robustus* is greater during the germination stage than during later stages of development (George 1980).

Little is known about the effects of specific ions on the two bulrushes. In otherwise suitable environments, total ionic content rather than concentrations of particular ions seems to determine whether *S. maritimus* occurs in prairie wetlands (Stewart and Kantrud 1972; Table 7). In wetlands in Saskatchewan and in other areas of the Great Plains, populations of *S. maritimus* thrive where sodium and magnesium ions reach high concentrations (Lieffers and Shay 1982b).

Wetlands that support the two bulrushes vary greatly in water chemistry (Table 8). *Scirpus maritimus* sometimes occurs in wetlands high in sewage effluents or nutrients (Chavan and Sabnis 1959; Kvet and Ondok 1973) and can withstand heavy contamination by oil (Stebbings 1970). Palmisano (1967) found no significant correlations between the distribution of *S. robustus* and alkalinity, hardness, or concentrations of magnesium, chloride, potassium, phosphorus, and calcium in Louisiana wetlands. Wilkinson (1970) found that this species grows best where water pH is less than 6.5, even though sediment pH may be much lower (to 3.1).

Fluctuations

Periodic occurrence of water or fluctuating water levels often characterize habitat of *S. maritimus* (Dodd et al. 1964; Hammer et al. 1975; Haslam et al. 1975; Hejny and Husak 1978; Husak and Hejny 1978). Bottom elevation, which in tidal wetlands controls the amount of aerial exposure required for the plant to attain high biomass, influences distribution (Hutchinson 1982; Karagatzides and Hutchinson 1991). In coastal British Columbia, *S. maritimus* occurs from the edge of the tidal flats far into the high marsh. This corresponds to an area that is submersed no more than about 60% of the time under normal tide conditions; biomass relative to other emerged plants is greatest in the zone submersed about 30% of the time (Hutchinson 1982). Plants that withstand wave action and flooding at each high tide tend to be much shorter than plants at slightly higher elevations (Stirrett 1954). About 80% of the aboveground production of *S. maritimus* may be carried away by tides and either deposited at higher elevations or removed to the estuary (Eilers 1975).

Populations of *S. maritimus* in inland waters also thrive under fluctuating water regimes. In the prairies, the frequency of occurrence of this bulrush sometimes increases greatly with gradual declines in water levels (Walker 1965). The rates of *S. maritimus* achene germination are higher in bottom cores from a Manitoba wetland subjected to artificial moist-sediment

Table 7. Relation of mean and range of water chemistry factors to abundance of *Scirpus maritimus* in prairie wetlands.[a]

Abundance rating (no. of wetlands)	Ca (mg/L)	Cl (mg/L)	SO$_4$ (g/L)	Alkalinity (mg/L CaCO$_3$) HCO$_3$	CO$_3$	pH
Occasional (2)	38	106	1.31	624	62	8.6
	(25-51)	(102-109)	(0.95-1.66)	(425-822)	(59-64)	(8.6-8.7)
Fairly common (15)	91	198	2.42	565	23	8.3
	(14-180)	(9-541)	(0.27-6.11)	(220-920)	(0-72)	(7.6-8.9)
Common (9)	145	554	4.59	536	14	8.0
	(15-346)	(94-1,250)	(2.16-9.84)	(252-977)	(0-54)	(7.4-8.4)
Abundant (8)	219	2,170	13.78	434	9	7.9
	(93-353)	(974-5,050)	(5.07-29.10)	(276-642)	(0-65)	(7.5-8.5)

[a] Unpublished data, Northern Prairie Science Center, Jamestown, North Dakota

Table 8. Chemical content of water in wetlands containing *Scirpus maritimus* or *S. robustus*.

Characteristic	Unit of measure	Range or single observation	Reference[a]
Scirpus maritimus			
pH and alkalinity system			
pH		6.4-9.7	1,2
Total alkalinity	mg/L $CaCO_3$	26-2,000	3,4
HCO_3 alkalinity	mg/L $CaCO_3$	39-977	5,6
CO_3 alkalinity	mg/L $CaCO_3$	0-216	7,5
Total hardness	g/L $CaCO_3$	0.1-20.2	8,6
Noncarbonate hardness	mg/L $CaCO_3$	57-3,700	9
Nutrient system			
Organic $N_{diss.}$	mg/L	0.17-4.34	10
NO_2-N	µg/L	0-84	10
NO_3-N	mg/L	0-23	11,12
NH_3-N	mg/L	0-99.8	5
$P_{diss.}$	mg/L	0.015-3.3	10
PO_4-P	mg/L	0-<22	11,13
K	mg/L	0.92-950	14,5
Other elements and compounds			
Al	mg/L	0-2	15
As	µg/L	9-200	9
B	mg/L	0.57-2.9	9
Ba	µg/L	100-200	9
Ca	mg/L	13-3,060	14,5
Cl	mg/L	0.4-18,000	10,5
Co	µg/L	0-2	9
Cr	µg/L	0-30	9
Cu	µg/L	0-180	9,15
F	µg/L	<50-500	5,7
Fe	mg/L	0.09-<40	7,14
Hg	µg/L	0.1-0.5	9
Li	mg/L	0.46-1.8	9
Mg	mg/L	0.9-9,518	10,5
Mn	µg/L	30-460	5
Mo	µg/L	3-16	9
Na	mg/L	5-50,400	10,5
Ni	µg/L	3-170	9,15
O2	mg/L	1.85-8.27	14,11
Pb	µg/L	3-10	9
S	mg/L	4.4	16
Se	µg/L	1	9
Si	mg/L	5-15	15
SiO_2	mg/L	0.1-<48	5,13
SO_4	g/L	>0.038-128.6	17,5
Sr	µg/L	410-970	9
Va	µg/L	4-14	9
Zn	µg/L	0.1-140	5,15
Scirpus robustus			
pH and alkalinity system			
pH		4.0-8.3	18,19
Total alkalinity	mg/L $CaCO_3$	140-890	20
Nutrient system			
Organic matter	%	0.08-0.79	19
$P_{diss.}$	mg/L	123-161	20
K	mg/L	1,708-4,373	20
Other elements and compounds			
Ca	mg/L	787-1,769	20
Cl	g/L	1.475-10.7	20,19
Mg	mg/L	2,617-3,327	20

[a] Where ranges list two reference numbers, left number applies to reference listing lowest value. References are: (1) Komarkova and Pribil 1973; (2) Lieffers 1984; (3) Sletten and Larson 1984; (4) White and Hartland-Rowe 1969; (5) consolidated data of Hammer et al. 1975, Hammer 1978, and Hammer and Heseltine 1988; (6) U.S. Fish and Wildlife Service, unpublished data; (7) Eisenlohr 1972; (8) Podlejski 1981; (9) U.S. Geological Survey 1976 to 1979, unpublished data, West Stump Lake, North Dakota; (10) Dykyjova 1986; (11) Olson 1979; (12) Shubert 1982; (13) Daborn 1975; (14) Kaul et al. 1978; (15) Kollman and Wali 1976; (16) U.S. Army Corps of Engineers 1984, unpublished data, West Stump Lake, North Dakota; (17) Willen 1962; (18) Chabreck 1972; (19) Beal 1977; (20) Palmisano and Newsom 1968.

conditions than in cores flooded with 2-3 cm of water Pederson 1983). Lieffers and Shay (1981, 1982a,b) show that populatioada in prairie Canada thrive where seasonal water levels fluctuate greatly, often a meter or more in the range 70 cm above to 40 cm below the sediment surface. This range is greater than that of several other emergents with which *S. maritimus* often associates in this area (Shay and Shay 1986). The abundance of *S. maritimus* declines under stable or rising water regimes, especially in less saline wetlands (Walker 1965; Millar 1973).

In Utah, stands of *S. maritimus* quickly establish when very shallow water flows across barren salt flats for 2-3 years (Nelson 1954). There, newly flooded salt flats dominated by *Salicornia* also develop persistent stands of *S. maritimus* and other emergents where depths of surface waters fluctuate up to 20 cm (Kadlec and Smith 1989).

Scirpus robustus is naturally adapted to fluctuating water levels. Philipp and Brown (1965) include *S. robustus* in a group of plants at least partially submerged with each daily tidal cycle. Sasser (1977) found this bulrush mostly in areas of Louisiana salt marshes that flood about 4,000-5,000 h/year during about 125-150 floodings/year, but concluded that the plant's occurrence was not strongly related to either the frequency or duration of flooding. In tidal wetlands, the duration of sediment submergence may affect the local distribution of this species more than depth of submergence, amounts and concentrations of sediment salts, water and organic matter content of the sediments, or seasonal changes in water salinity (Mall 1969).

Scirpus robustus seems to grow best where tidal amplitudes are less than 1 m (Palmisano and Newsom 1968; Flowers 1973), although this may be modified by wind speed and direction and by flow from adjacent rivers (Hackney and Cruz 1982). (See the sections on propagation and management for more information on the effects of water-level fluctuations on this species.)

Bottom Sediment

Texture

Differences in sediment texture are associated with variations in sediment salinity and degree of waterlogging, that are important environmental variables in salt marshes (Brereton 1971). Of 27 references to sediment texture in habitats supporting *S. maritimus*, most list clay (Table 9). Several of these references also list muds which are presumably high in organic matter. More than half of the references for *S. robustus* list organic sediments.

Walker and Coupland (1970) surveyed vegetation on a variety of sediment types based on texture, organic content, and water-holding capacity. They found nearly all stands of *S. maritimus* on sticky alkaline clay. Ranwell (1972) identified clays with higher cation exchange capacities (10-40 mE) as favoring good growth of this bulrush, but he noted that the higher capacities also indicate increased concentrations of nutrients and calcium. Klavestad (1957) observed the most well developed stands of this species along estuarine shores where clays have inputs of freshwater. However, freshwater inputs may be less important where *S. maritimus* grows on peats (Jacobson and Jacobson 1989). Adam (1981) and Ewing (1986) described optimum substrates for *S. maritimus* as soft and anoxic or highly reduced. Moody (1978) noted especially high rates of pioneering on silts.

Several authors suggest that sediment texture is insignificant for *S. maritimus* or note that the species grows in a wide variety of sediment textures (Dix and Smeins 1967; Haslam et al. 1975; Looman 1981).

Barko et al. (1977) grew *S. robustus* on a variety of dredge spoils in a greenhouse and found much higher biomass of plants grown in clay than those grown in sand, probably because of its lower nutrient (N, P) content. They had no success growing this species in spoils that were mostly silty clay, probably because they had much higher free-water salinities. Baden et al. (1975) reported that *S. robustus* is mostly found on silts, but that sediment texture seemingly is unimportant. Dominance of *S. maritimus* on sandy or other easily eroded bottom sediments may depend on the intolerance of other plants to the erosive effects of wave or ice action at such sites (Tyler 1969).

In summary, predominantly clay sediments support most natural stands of *S. maritimus*, whereas clays and organic sediments support most stands of *S. robustus*. Nonetheless, in the absence of other limiting factors, both bulrushes probably can grow on all common textural types, except possibly on rubble, boulder, and stone.

Sedimentation and Disturbance

Scirpus maritimus invades silted tidal ponds in British Columbia and Oregon (Jefferson 1974; Moody 1978; Hutchinson 1982). These ponds accumulate silt after other emergents reduce tidal energy. *Scirpus maritimus* is also characteristic of emerging flats in European maritime areas undergoing land upheaval (Dijkema et al. 1984). *Scirpus maritimus* is exclusively an invader of mudflats in Oregon salt marshes; disjunct stands are rare at such sites (Eilers 1975). Seed production in these marshes is uncommon,

Table 9. Predominant textural types of bottom sediments supporting growth of *Scirpus maritimus* and *S. robustus.*[a]

Reference	Clay	Silt	Sand	Loam	Organic[b]
Scirpus maritimus					
Klavestad 1957	x				
Ungar 1965			x		
Walker 1965	x	x			
Smeins 1967	x		x		
Ungar 1967	x				
Ungar 1968	x				
White and Hartland-Rowe 1969	x				
Walker and Coupland 1970	x				
Lundegardh-Ericson 1972					x
Ranwell 1972	x				
Jefferson 1974		x			
Haslam 1978	x		x		
Hejny and Husak 1978	x				
Husak and Hejny 1978b	x				
Kaul et al. 1978	x				
Olson 1979		x			
Britton and Podlejski 1981	x	x			
Podlejski 1981	x				
Lieffers and Shay 1982b	x		x	x	
Fulton et al. 1983	x				
Jerling 1983	x				
Ferrari et al. 1985			x		
Dykyjova 1986	x			x	
Palmer 1986	x				
Van Wijk 1988	x				
Jacobson and Jacobson 1989					x
Kikuchi et al. 1989			x		
Karagatzides and Hutchinson 1991		x	x		
Scirpus robustus					
Johannessen 1961b	x				
Philipp and Brown 1965	x				
Walts 1967					x
Palmisano 1970					x
Flowers 1973					x
Baden et al. 1975		x			
Reimold 1977					x

[a] Texture of uppermost strata only. In some cases, these are as shallow as 5 cm.

[b] Includes fibric (peat), hemic (muck), and sapric (sapropel or gyttja).

probably because of excessive inundation periods. Although the distribution of *S. maritimus* in British Columbia may be controlled primarily by sediment moisture and salinity, invasion may be greatest where vegetation traps fine particles and raises sediment moisture (Hutchinson 1982). Stands of *S. maritimus* in erosional and depositional zones in Czechoslovakian impoundments differ mainly in stand density rather than height (Dykyjova 1986). Protection from wave action increases corm survival, but the effects of sediment deposition on corms are unknown (Foote 1988).

Both bulrush species flourish in severely disturbed sites such as blasted wetlands (Warren and Bandel 1968); borrow pits, canals, drainage ditches, and dredged spoil deposits (Palmisano and Newsom 1968; Palmisano 1970; Adam 1981; Newling et al. 1983; Palmer 1986); and ponds in coal strip-mines (Olson 1979; Fulton et al. 1983). Both species also grow in areas disturbed by agriculture (Smeins 1967; Bassett 1978; Podlejski 1981, 1982; Pederson and Van der Valk 1984; Ferren 1985) or construction (Nelson 1954; Ranwell 1972; Wolseley 1986; Krahulec et al. 1987; Capehart and Hackney 1989; Brostoff and Clarke 1993). *Scirpus robustus* naturally colonizes new deltas formed by floods (Fuller et al. 1985). Storm tides may be instrumental in the perpetuation of this species in coastal Louisiana, although severe hurricanes sometimes eliminate stands for at least a year (Beter 1957; Kimble 1958; Chabreck and Palmisano 1973). In the Phillipines, Bernasor and DeDatta (1986) found greater *S. maritimus* stem density in continuously wet rice fields than in farmed fields on alternate wet and dry regimes.

In summary, sexual reproduction and seedling establishment in these bulrushes are strongly related to the availability of unvegetated sediments. Both species are highly tolerant of natural and artificial disturbances to bottom substrates, although little is known about adaptations to such stresses.

Chemistry

Scirpus maritimus grows on saline sediments and on sandy beach ridges where salinities are low (Flowers 1934; Tsopa 1939, cited in Chapman 1974; Penfound 1953; Ferrari et al. 1985). Plants occupy wetlands with sediment interstitial water conductivities ranging from 1.3 to 120 mS/cm and with as much as 6.3% dry weight total salts (Table 10). More robust stands are usually where conductivities range from about 4 to 23.0 mS/cm (Smeins 1967; Lieffers and Shay 1982a; Ewing 1986) and sediments contain about 0.3-1.0% dry weight total salts (Ungar 1965). Plants may not produce achenes in well-drained, highly saline sediments (Ungar 1970). In prairie Canada, plants are absent from wetlands where interstitial water conductivities exceed 40 mS/cm and water tables regularly fall well below the sediment surface (Looman 1981). However, where water tables remain high, short sterile plants can survive for several years at conductivities three times higher. In Saskatchewan, populations of *S. maritimus* grow in saline gleysols where highest salt content occurs in the upper 30 cm (Dodd and Coupland 1966b). Production experiments with *S. maritimus* in sediment with added sodium chloride show maximum corm numbers at 5.6-6.9 mS/cm and maximum corm weights at 4.6-5.6 mS/cm (Mercado et al. 1971). Bassett (1978) showed that *S. maritimus* ranks fourth in mean sodium tolerance among the 38 most frequent species in a Camargue (France) pasture.

In the Canadian prairies, current- and previous-year water levels and salinity, rather than the ionic concentrations in bottom sediments, show best correlations with *S. maritimus* plant size, seed production, and density (Lieffers and Shay 1982b). In wetlands in this region, achenes germinate and seedlings grow on wet mudflats if sediment salinities are less than 20 mS/cm (Lieffers and Shay 1982b). Vigorous stands regularly occur in some of these wetlands when surface water is present during the growing season, because salts move from sediments to the water column. Stand establishment is greatly inhibited in other wetlands where salt content of sediments does not decrease when surface water is present and where water salinities continue to increase, probably because of inputs of saline groundwater. Under continuous flooding, such high salinities, particularly in central areas, can preclude the growth of any emergent hydrophytes (Lieffers and Shay 1983).

Scirpus maritimus usually occurs where sediment pH varies from 5.2 to 8.9 (Table 10), although an acidophilous subspecies in Europe grows where sediment pH is as low as 3.7 (Husak and Hejny 1978; Dykyjova 1986).

Sediments for *S. maritimus* are often described as eutrophic or high in organic matter (Daborn 1975; Haslam et al. 1975; Looman 1981). *Scirpus maritimus* biomass is markedly higher on nutrient-rich sediments, even though the plant is less influenced by nutrient availability than several other common genera of emergent hydrophytes (e.g., *Phragmites, Glyceria, Sparganium,* and *Typha*; Dykyjova 1986). Bassett (1978) found more robust stands of *Scirpus maritimus* in areas high in organic matter, potassium, and organic nitrogen but relatively low in pH. Podlejski (1981) found positive correlations between the number of leaves per stem and the total sediment nitrogen; leaf area-to-weight ratios correlated with amounts of sediment organic matter. High correlations between total nitrogen and organic matter suggest that high concentrations of both substances lead to plants with thicker stems and broader leaves (Podlejski 1981).

Karagatzides and Hutchinson (1991) found that the greater standing crops of *S. maritimus* on high marsh compared to low marsh more strongly correlated with the number of daylight hours of tidal exposure than with any of a wide variety of physical and chemical sediment variables. However, they noted that the length of tidal exposure may also relate to the chemical variables. For example, high marsh may yield large crops where decaying wrack raises levels of nitrogen and other nutrients, whereas the less exposed low marsh may have small crops because of reduced sediment nitrogen and greater potential for the production of toxic sulfides. Young corms may be especially vulnerable to sulfide poisoning if saline lakes flood during midsummer (Lieffers 1981).

Table 10. Chemistry of bottom sediments supporting *Scirpus maritimus* and *S. robustus.*[a]

Characteristic	Unit of measure[b]	Range or single observation	Reference[c]
S. maritimus			
Conductivity	mS/cm	1.3-120	1,2
Total salts	% d.w.	0.29-6.3	3,4
pH		5.2-8.9	5,6
Major nutrients			
K	% d.w.	<0.01-1.74	7,5
K	mg/L	141-340	8,9
N	% d.w.	0.03-2.34	10,11
N	mg/L	3.3-36.5	9
P	% d.w.	0.002-0.18	10,11
P	mg/L	1-2	9
Organic C	% d.w.	0.89-17.8	7
Organic matter	% d.w.	3.5-54	12,13
Organic matter	% loss on ignition	7.0-18.0	14,15
Other elements and compounds			
Al	% d.w.	7.12-8.12	11
Ca	% d.w.	<0.02-3.16	16,11
Ca	g/L	0.16-1.59	9
Cl	% d.w.	<.002-1.08	5,17
Cl	mg/L	21.26	16
Cu	µg/g d.w.	41.6->125	5
Cu	mg/L	4.13	16
Fe	% d.w.	2.96-8.28	11,5
Fe	mg/L	100.35	16
H_2O	% d.w.	24.0-48.4	10,19
Mg	mg/g d.w.	0.04-6.7	7,11
Mg	mg/L	120-839	9,8
Mn	mg/g d.w.	0.29-0.51	5
Mn	mg/L	373	16
Na	mg/g d.w.	0.03-7.0	7,19
Na	g/L	0.62-2.20	9,20
S	% d.w.	0.84-0.97	5
SO_4	% d.w.	0.1-0.6	19,18
SO_4	mg/L	0.10-976.2	9,16
Zn	µg/g d.w.	85-395	5
Zn	mg/L	1.57	16
Scirpus robustus			
Conductivity	mS/cm	2.6-111	21,22
pH		3.1-6.6	22,23
Major nutrients			
K	mg/L	270-867	24,25
N	% d.w.	0.64-0.80	26,25
NH_4-N	mg/L	95	25
NO_3-N	mg/L	4.6	25
P	mg/L	1.5-50	27,24
C	% d.w.	9.47-13.02	26,24
Organic matter	% d.w.	11.9->40	25,28
Other elements and compounds			
Ca	g/L	0.15-2.30	26,25
Cu	mg/L	5.7	25
Mg	g/L	0.48-4.15	27,25
Mn	mg/L	25	25
Na	g/L	3.32-20.48	26,25
Zn	mg/L	21	25

[a] Wet measures are from sediment extracts at different dilution ratios. If results were reported from different sediment levels, the upper-level figures were used. Salinity was converted to conductivity with the following multipliers: 0-2 g/L x 1.43; 2-40 g/L x 1.0; >40 g/L x 0.67.

[b] mS/cm=millisiemens/cm, d.w.=dry weight.

[c] Where ranges list two reference numbers, the left number applies to reference listing lowest value. References are: (1) Smeins 1967; (2) Looman 1981; (3) Ungar 1965; (4) Nienburg and Kolumbe 1931, cited in Chapman 1974; (5) Karagatzides and Hutchinson 1991; (6) Nelson 1954; (7) Dykyjova 1986; (8) Dodd et al. 1964; (9) Podlejski 1981; (10) Kikuchi et al. 1989; (11) Kaul et al. 1978; (12) Yamanaka 1975; (13) Walker 1965; (14) Ungar 1968; (15) Bassett 1978; (16) Olson 1979; (17) Ungar 1967; (18) Ungar 1970; (19) Ungar et al. 1969; (20) Mercado et al. 1971; (21) Soileau 1966; (22) Wilkinson 1970; (23) Palmisano and Newsom 1968; (24) Chabreck 1972; (25) Linthurst and Seneca 1980; (26) Palmisano 1970; (27) Prevost and Gresham 1981; (28) Mall 1969.

Sediments supporting *S. robustus* are in saline and brackish wetlands (Palmisano 1970; Stalter 1973; Baden et al. 1975). Stands occur where interstitial water conductivities vary from 2.6 to more than 100 mS/cm (Table 10), but the optimum range seems to be about 4-28 mS/cm (Palmisano and Newsom 1968; Mall 1969; Palmisano 1970; Chabreck 1972). Plants at highest salinities probably are dormant (Miller 1962). The limit of sediment osmotic potential for *S. robustus* is about -3.5 MPa (Ustin et al. 1982).

Of 12 sediment and water chemistry variables studied by Palmisano (1967) in Louisiana wetlands, only sediment salt concentrations significantly correlated with the distribution of *S. robustus*. Most robust stands there occur where salt concentrations average about 15 mg/L. Mall (1969) considered sediment salt concentration the second most important factor, after length of sediment submergence, controlling the distribution of hydrophytes in a California wetland. There, aboveground biomass of *S. robustus* is highest where sediments are submerged for 7 to 8 months, mean annual sediment salt concentrations range from 8.6 to 28.0 g/L, and sediment organic matter is more than 40%. Mall (1969) noted that when mean annual salt concentrations in the sediments fall below 8 g/L, the number of plants is reduced, although growth rate remains high. Germination of *S. robustus* achenes is best in sediments with soluble salt concentrations of 9 g/L or less (Prevost and Gresham 1981). Mall (1969) noted greatest achene yields on sediments of 9.3 g/L salinity submerged for 7 months. However, Pearcy et al. (1982) and Pearcy and Ustin (1984) noted that this species competes best where salinities increase from spring to summer. They found no clear relation between achene production and salinity from year to year and questioned the predictive value of simple regressions between various production measurements and salinity.

Wilkinson (1970) grew *S. robustus* where sediment pH falls as low as 3.1, but where water pH remains 6.5 or higher. Prevost and Gresham (1981) found best achene germination where sediment pH ranges from 5.1 to 5.7. The ranges in concentrations of other chemicals in sediments supporting the two bulrushes are listed in Table 10.

Slope

The only information on the effect of slope on either of the two bulrushes seems to be that of Klavestad (1957), who found *Scirpus maritimus* restricted to bottoms that slope 10 degrees or less.

Land Use

Wetlands supporting *Scirpus maritimus* are often grazed by livestock (Brehm 1979; Sykora et al. 1987; Westhoff 1979; Jerling 1983; Fulton et al. 1986). This bulrush usually replaces presumably more palatable emergents (Klavestad 1957; Britton and Podlejski 1981; Grillas and Duncan 1986). Podlejski (1981, 1982) found higher root-to-shoot ratios and lower underground biomass of *S. maritimus* in grazed, monotypic stands. Plants are most readily consumed by livestock in early summer when shoots are short and soft (Tyler 1969). Although mean stem densities usually decrease with heavy grazing, such grazing during the growing season usually results in stands of short, nonflowering plants; these stands may have greater stem densities than ungrazed stands (Bassett 1980; Duncan and D'Herbes 1982).

Grazing in northern European salt marshes favors the replacement of *S. maritimus* and *Phragmites australis* with *Puccinellia maritima* and *Agrostis stolonifera* (Beeftink 1977). *Scirpus maritimus* can temporarily increase in heavily grazed wetlands if grazing ceases (Coetzer 1987), but under such idle conditions, taller emergents such as *Phragmites australis* probably completely replace this bulrush in as little as 10 years (Pehrsson 1988). Submersed plants can replace *S. maritimus* in deeper wetlands that are intensively grazed (Grillas and Duncan 1986).

Natural herbivores, such as muskrats (*Ondatra zibethicus*), can consume competing emergents and increase the abundance of *S. maritimus* (McCabe and Wolfe 1988). However, grazing geese, ducks, and other waterbirds, especially along exposed shorelines, can greatly reduce the abundance of this bulrush (Fiala and Kvet 1971). Stands of *S. maritimus* can be destroyed if grazing by geese that forage on the corms is combined with long-term grazing by livestock (Olsen 1945; Pehrsson 1988).

Scirpus maritimus often inhabits cultivated areas (Visperas and Vergara 1976a; Bassett 1978). In Saskatchewan, plants flourish in wet meadows of moderate salinity that are occasionally rather than frequently cultivated (Walker and Coupland 1970).

Burning of dry stands of *S. maritimus* can significantly reduce the number of rhizomes in the upper 10 cm of the bottom substrate yet have little effect on vegetative reproduction (Smith, L. 1983). This bulrush occurs in areas formerly dominated by other emergents after draining, burning, and reflooding (Smith and Kadlec 1985b). Stands burned in fall attract avian and mammalian herbivores that reduce standing crops

(Smith and Kadlec 1985c). Along the Texas gulf coast, fires in fall and winter expose corms and initiate new growth that is eagerly consumed by wintering geese (Stutzenbaker and Weller 1989). However, in more northerly areas, fires may destroy achenes that wintering waterfowl may otherwise obtain from inflorescences that protrude through the ice (Wetmore 1921). Palmisano (1967) placed *S. robustus* achenes in a wetland dominated by this species and burned the vegetation in the wetland a few days later. He found slight but probably nonsignificant increases in the speed with which achenes subject to fire germinate. However, he concluded that the results could have been much different had the moisture content of the wetland bottom been lower and the peat layer also burned. Smith et al. (1984) found no increases in protein content of *S. maritimus* after burning.

Mowing often increases dominance or frequency of *S. maritimus* (Walker and Coupland 1970; Britton and Podlejski 1981; Cowie et al. 1992) but may gradually decrease shoot length or weaken plants (Vestergaard 1985). Palmer (1986) found the frequency of occurrence and the cover percentage were greater for *S. maritimus* than for taller emergents in cleared ditches. Mowing with removal of vegetation before reflooding reduces *S. maritimus* biomass more than burning, probably because of the lack of a nutrient pulse from the ash (Smith and Kadlec 1985d). Culture experiments show that cutting of 110- to 140-day-old shoots of this bulrush induces the emergence of inflorescences, but earlier cutting and noncutting of controls do not (Visperas and Vergara 1976c). The reasons for this phenomenon are unknown.

Less is known about the effects of common land use practices on *S. robustus*. Livestock are excluded from some tidal wetlands that support this bulrush because of large tidal amplitudes (Latham et al. 1994). Davison and Neely (1959) considered cattle grazing favorable to this bulrush in the southern United States. However, of the eight most common plants in a large California marsh, Mall (1969) found unsubmerged *S. robustus* the most vulnerable to damage by cattle grazing. Management to improve stands of *S. robustus* with cattle is difficult because the animals eat the seedheads and vegetative parts (George 1980). In a Florida wetland, *S. robustus* appeared after a dense stand of *Juncus roemerianus* was mowed, but the area was also grazed by cattle (Myers 1956). The percent cover of *S. robustus* increases after grazing by wintering geese in North Carolina and decreases when the birds are excluded (Smith, T. 1983). When Louisiana wetlands dominated by this bulrush are heavily grazed by wintering geese, the value of these wetlands for livestock grazing and muskrat trapping declines (Lynch et al. 1947).

Fire in stands of *Spartina patens* in Louisiana wetlands often increases *Scirpus robustus* or *S. olneyi* (Penfound and Hathaway 1938; Lay and O'Neil 1942; Wells 1942). With no further disturbances, other emergents largely replace these bulrushes within 1 to 2 years (Beter 1957). Whipple and White (1977) noted that although *S. robustus* appears after fires in these wetlands, the order of importance of the original dominant species remains unchanged. They attributed this resiliency to the long history of periodic fires in these wetlands. Louisiana landowners commonly burn wetlands to attract waterfowl, facilitate travel, and improve livestock grazing, but the resultant plant species composition depends on water depths, tides, and weather after burning (Hoffpauer 1968). In South Carolina, waterfowl increase their use of *S. robustus* when wetlands that support dense stands are drained, burned, and reflooded in late winter (Loesch et al. 1989). Wetlands burned in strip patterns during January and then flooded with 20-25 cm water seem to attract the most birds (R. K. Williams, Kinloch Plantation, Georgetown, South Carolina, personal communication). Established stands of *S. robustus* in California are mowed in August to reduce rankness and aid in control of *Typha* (Connelly 1979).

Biotic Communities and Associated Limiting Factors

Macrophytes

Scirpus maritimus and *S. robustus* often occur in pure stands (Keith 1961; Hyer 1963; Palmisano 1970; Eilers 1975; Adam 1981; Shay and Shay 1986) that occupy discrete elevational zones (Verhoeven 1980; Jacobson and Jacobson 1989). These bulrush species have physiological mechanisms that enable them to prosper in moderately saline environments and survive when salinities increase past the point tolerated by many other vascular hydrophytes. Laboratory cultures show high germination and growth in freshwater, especially by *S. robustus*, but the ability of both species to compete in nature with glycophytes in freshwater seems low. Compared with some of their potentially important competitors, *S. maritimus* and *S. robustus* probably survive better in nutrient-poor sediments or exposed sites. The two bulrushes are shallow-water plants, intolerant of flooding for extended periods but adapted to survive low water levels, periodic exposure of bottom substrates, and drought. Achenes of both bulrushes disperse widely, allowing pioneering by sexual reproduction on bare substrates when moisture conditions permit. Nevertheless, compared to many other emergent hydrophytes, these bulrushes are relatively short, and competition, especially for light, seems to be an important factor in their spatial and temporal distribution.

Despite these limitations, *S. maritimus* and *S. robustus* commonly coexist with many other emergent hydrophytes. For example, as many as 72 other species of vascular plants may occur on small (generally 2 × 2 m, but some larger) plots with *S. maritimus* in British salt marshes (Adam 1981). *Scirpus maritimus* has a much wider distribution, a more extensive literature, and consequently a much longer list of associated species (Appendix A) than *S. robustus* (Appendix B). Although the information in these appendixes does not reflect a random sample of the habitat of the two bulrushes, species or genera showing high frequency of association with them may be important competitors in managed wetlands. However, most species listed in these tables are not serious competitors. Examples of the latter are ground-layer species or vernal species that mature earlier than *S. maritimus* (Handoo and Kaul 1982). Also, neither positive nor negative associations imply anything about competition, which is difficult to prove even in controlled environments.

Based on sources in Appendix A, two groups of plants are the most frequent associates of *S. maritimus*. The first includes much taller, often long-lived perennial graminoids—especially *Phragmites australis*, *Typha latifolia*, *S. acutus*, and *S. tabernaemontani*—that often shade out *S. maritimus*. Although some of these plants have a tendency toward halophytism, their height alone probably provides a competitive advantage over *S. maritimus* in deeper, more permanently flooded wetlands (Nelson 1954; Stewart and Kantrud 1972; Shay and Shay 1986; Kantrud et al. 1989). The number of emergent species associated with *S. maritimus* decreases with increasing water depth (Reinink and Van der Toorn 1975). Small increases in water depth for most of the year enable the more aggressive *Phragmites australis* and *Typha latifolia* to shade out stands of *S. maritimus* in Czechoslovakian fish ponds (Fiala et al. 1968; Fiala and Kvet 1971). Competition for sunlight probably allows *Phragmites australis* to replace *S. maritimus* in the absence of grazing by horses in the French Camargue (Duncan and D'Herbes 1982). Similarly, idle, ungrazed conditions may cause stands of *Typha* spp. and *S. acutus* to replace *S. maritimus* in many northern Great Plains wetlands (Kantrud et al. 1989). Conversely, *S. maritimus* may invade wetlands when *Typha* is reduced (Nelson and Dietz 1966).

The second group of frequent associates of *S. maritimus* includes *Triglochin maritima*, *Eleocharis palustris*, *Atriplex patula*, *S. americanus*, *Hordeum jubatum*, and several species of *Juncus*. These plants are similar to *S. maritimus* in height and show strong halophytic tendencies. Increases or decreases in the competitive advantage of these species over *S. maritimus* are to be expected with subtle changes in salinity, elevation, disturbance and inundation regime, substrate texture, and many other factors (Ranwell 1961; Hyer 1963; Dodd and Coupland 1966b; Walker and Coupland 1970; Eilers 1975; Hutchinson 1982; Ewing 1983; Vince and Snow 1984; Shay and Shay 1986; Price et al. 1988). Bolen (1964) noted invasion of *S. acutus*, *S. olneyi*, *Distichlis spicata*, and *Eleocharis rostellata* in a relict community of *S. maritimus* surviving under abnormally low soil salinity and presumed the eventual elimination of the community. The hybrid *Spartina townsendii*, discovered in England in 1870, can eliminate *Scirpus maritimus* (Oliver 1925). Similarly, stands of the introduced *Spartina patens* in Oregon wetlands are expected to replace the native *Deschampsia cespitosa-Scirpus maritimus* community (Frenkel and Boss 1988). Conversely, introduced or adventive populations of *S. maritimus* sometimes replace native emergent species in Australia (Congdon 1981).

Stands of *S. maritimus* also frequently intersperse with submersed and floating angiosperms, especially with *Lemna* spp., *Potamogeton pectinatus*, *Ranunculus* spp., *Ruppia* spp., *Spirodela polyrrhiza*, and *Zannichellia palustris* (Metcalf 1931; Jensen 1940; Walker and Coupland 1970; Stewart and Kantrud 1971; Chapman 1974; Molinier and Tallon 1974, cited in Podlejski 1981; Riley and McKay 1980; Britton and Podlejski 1981; Lieffers 1981; Rejmankova 1978; Grillas and Duncan 1986). Several of these species, particularly *Ruppia* spp. and *Zannichellia palustris*, often fill in gaps in stands of *Scirpus maritimus* created by mowing, grazing, or ice scour (Tyler 1969).

Frequent associates of the coastal-dwelling *S. robustus* are the salt-tolerant graminoids *Distichlis spicata*, *Spartina alterniflora*, *S. cynosuroides*, *S. patens*, and *Scirpus olneyi* (Appendix B). All except *Distichlis spicata* are similar in height to or taller than *S. robustus*. Of the major emergent hydrophytes in coastal Louisiana wetlands, *Distichlis spicata* shows the strongest association with *S. robustus*, but its major competitor is *Spartina patens* (Palmisano 1970). This deep-rooted species tolerates a greater range of salinities and water levels than *Scirpus robustus*. Thus, standard management for increasing amounts of *S.*

robustus may not be suitable in wetlands dominated by *Spartina patens* (Palmisano 1970). The most common submerged and floating associates of this bulrush are *Ruppia maritima, Myriophyllum spicatum,* and *Lemna minor* (Palmisano 1970; Chabreck 1972; Kelley and Porcher 1986).

Chapman (1974) provided information on ecological succession in salt marshes worldwide as elevations increase or decrease through accretion or subsidence. He considered maritime salt marshes essentially developmental, with accumulations of soil and organic matter leading to drier, less saline wetlands shoreward. Under this concept, maritime wetland communities with *Scirpus maritimus* as a dominant usually develop at intermediate elevations and salinities on mudflats or where the submergents *Ruppia, Zostera,* or *Zannichellia*, or the emergent *Spartina* were formerly dominant. In turn, communities dominated by *Phragmites, Carex,* or *Juncus* usually replace the communities where *Scirpus maritimus* dominates (Johannessen 1961a; Van Donselarr et al. 1961; Ranwell 1964; Flowers 1973; Chapman 1974; Jefferson 1974). For inland (Nebraska) wetlands, Ungar et al. (1969) outlined a hypothetical succession based on reduced salinity and lowered water levels. They suggested that a *S. maritimus*-dominated community could succeed communities of submersed (*Ruppia*) or emersed (*Salicornia*) species. Communities dominated by *Hordeum* or *Iva* species or *Distichlis spicata* could then replace the *Scirpus maritimus* community when water levels or salinities fall, or the sites could revert to bare salt pans in a cyclical pattern if salinity and moisture levels stabilize.

Algae

Stands of *Scirpus maritimus* frequently contain the macroalgae *Chara* spp. and *Enteromorpha* spp. (Metcalf 1931; Jensen 1940; Nelson 1954; Klavestad 1957; Stewart and Kantrud 1971; Daborn 1975; Britton and Podlejski 1981; Lieffers 1981; Grillas and Duncan 1986). A carpet of *Vaucheria* frequently covers the bottom in Swedish stands (Tyler 1969). Marvan and Komarek (1978) described stands of *S. maritimus* as poor in epiphytes but rich in planktonic and filamentous algae. Marvan et al. (1978) suggested that greater light penetration increases the frequency of planktonic algae more in the shorter, more open stands of *S. maritimus* than in stands of taller emergents such as *Phragmites australis, Schoenoplectus (Scirpus) lacustris,* and *Typha latifolia.* The alga *Vaucheria* sometimes helps stabilize soft silts between *S. maritimus* shoots (Gillham 1957). *Cladophora* spp. may be abundant algae during the first year South Carolina impoundments are flooded but may disappear as populations of *S. robustus* and *Ruppia maritima* expand (Wilkinson 1970). DeVoe and Baughman (1986) quantified algal taxa in planktivorous fishes from South Carolina impoundments that support *S. robustus.* Zingmark (1986) measured productivity of microbenthic algae from those impoundments. Komarkova and Marvan (1978) estimated annual and gross productions of planktonic and periphytic (including filamentous) algae in a Czechoslovakian *S. maritimus* stand. Algal associates of this bulrush in wetlands in Russia (Gladyshev and Kogan 1977) and the Netherlands (Verhoeven and Van Vierssen 1978) are listed.

Diseases and Parasites

Little is known about pathogens or parasites of the two bulrushes. Clevering et al. (1995) noted mortality of *Scirpus maritimus* caused by *Pseudomonas* bacteria in the greenhouse but not of infected plants in the field. The fungus *Uromyces lineolatus* parasitizes *S. maritimus* in England (Ellis 1960, cited in Beeftink 1977). Two recently described nematodes form root galls on California populations of *S. robustus* (Abdel-Rahman and Maggenti 1981a,b; 1987a,b).

Invertebrates

Primary invertebrate groups found in the digestive tracts of waterfowl collected in stands of *Scirpus maritimus* in coastal Oregon are Cladocera, Copepoda, Ostracoda, Odonata, Chironomidae, and Molluska (Pederson and Pederson 1983). Stands in extremely saline lakes in interior Canada may support few benthic invertebrates, although certain crustaceans often are abundant (White and Hartland-Rowe 1969; Daborn 1975; Hammer et al. 1975). In Galveston Bay, Texas, Rozas and Zimmerman (1994) recorded higher densities of several decapod crustaceans in stands of *S. maritimus* than in other habitat types. In New Jersey, *S. maritimus* is a major species used by a dipteran (*Hybomitra daeckei*) for ovipositing (Sofield and Hansens 1982).

Consumption of *S. maritimus* by invertebrates seems common. Lepidopteran caterpillars may remove 46% of the standing crop in Utah wetlands (Foote et al. 1988). At least eight specialized endophagous invertebrates are known from stands in western Europe (Dijkema et al. 1984). Syrphid flies feed on *S. maritimus* pollen in the Netherlands and may aid in pollination (Leereveld et al. 1981; Leereveld 1984).

Invertebrates have been described from wetlands that support this bulrush in California (Schuler 1987), Korea (Kikuchi et al. 1989), and the Netherlands (Verhoeven and Van Vierssen 1978; Smit et al. 1981, cited in Adam 1990; Dijkema et al. 1984). Powell et al. (1987) identified substances in *S. maritimus* that are toxic to brine shrimp.

Of various sampling sites in natural wetlands and impoundments in South Carolina, sites in impoundments dominated by *S. robustus* have the highest densities of macrobenthic invertebrates, especially Oligochaeta, Molluska, Polychaeta, and Insecta (Wenner and Beatty 1988). Coull (1986), DeVoe and Baughman (1986), Olmi (1986), Taniguchi (1986), and Wenner (1986a,b) documented the species compositions and abundances of planktonic, benthic, and nektonic organisms in these wetlands. These impoundments can be used for the commercial culture of various crustaceans (Wenner and Beatty 1988). Fiddler crabs (*Uca minax*) attain high populations in coastal Virginia wetlands dominated by *S. robustus* (Kerwin 1971). Ditching portions of Delaware wetlands dominated by *S. robustus* for mosquito control eliminates shallow water and reduces populations of macroinvertebrates important as foods of waterbirds (Bourn and Cottam 1939, 1950; Cottam et al. 1938; Daiber 1974).

Amphibians, Reptiles, and Fishes

Little information is available on the use of the two bulrushes by amphibians, reptiles, or fishes. Alligators (*Alligator mississippiensis*) regularly use South Carolina impoundments containing stands of *Scirpus robustus* (Epstein and Joyner 1986). These wetlands can support commercial fisheries (Wenner et al. 1986; Wenner and Beatty 1988). Seeds of *S. maritimus* are consumed by common carp (*Cyprinus carpio*) in France (Crivelli 1981).

Birds

Plants in the genus *Scirpus* provide food and cover for many aquatic birds (Martin et al. 1951; Haslam 1973). Stands of *S. maritimus* and *S. robustus* on managed and unmanaged wetlands rate especially high as sources of plant and animal food and as cover for moulting, migrating, and wintering waterfowl (Wetmore 1921; Chamberlain 1959; Yocom and Keller 1961; Wilkinson 1970; Palmisano 1972; Morgan et al. 1976; Sandifer et al. 1980; Gordon et al. 1987; Gray et al. 1987; Strange 1987; Thorn and Zwank 1993).

Certain groups of waterfowl eat the two bulrushes; dabbling ducks especially consume the achenes (Table 11). Addy (1946) considered *S. maritimus* superior to *S. robustus* for migrant American black ducks (*Anas rubripes*) in Massachusetts because *S. maritimus* is shorter and its heads shatter achenes earlier. Mallards (*A. platyrhynchos*) may prefer wetlands where managers increase the availability of *S. robustus* achenes through winter burning (Loesch et al. 1989). Hurricanes probably have minor effects on the availability of achenes for ducks (Kimble 1958; Kimble and Ensminger 1959).

Although ducks frequently consume them, the importance of achenes as food remains obscure because they may also serve as grit (Mall 1969; Pederson and Pederson 1983). Also, *S. robustus* achenes rank low in preference when offered to various ducks, geese, and American coots (*Fulica americana*) *ad libidum* with six other domestic and wild seeds and commercial chicken feed (McFarland et al. 1963). Large numbers of achenes pass through the digestive systems of some waterbirds with increased viability and can be transported long distances (DeVlaming and Proctor 1968; Ogle 1981).

Shoots, rhizomes, and corms of both bulrushes are readily eaten by geese (Table 11). Their grubbings sometimes heavily damage large stands of *S. maritimus*, but such stands have great regenerative capacity and may benefit from the openings created (Nagel 1969; Zwarts [1972] and Loosjes [1974], cited in Reed 1989; Ondok and Kvet 1978). Goose grubbing can greatly reduce belowground net production of both *S. robustus* and *S. maritimus* (Smith and Odum 1981). Nevertheless, grubbed stands sometimes increase their canopy covers because of increased achene production and seedling growth when environmental conditions are favorable (e.g., high rainfall that reduces bottom substrate salinity, and lack of high tides that can damage stands; Smith, L. 1983). Where geese are excluded from such sites, *S. robustus* can decrease under competition from other rhizomatous emergents such as *Spartina patens* (Smith, T. 1983). Wintering geese can have drastic effects on stands of *Scirpus robustus*. Intense feeding by large numbers of geese sometimes deepens wetlands, causing their abandonment as livestock pasturage (McAtee 1910; Lynch et al. 1947). If storm tides follow and remaining vegetation is washed away, open-water lakes are created that can persist for decades (McAtee 1910; Lynch et al. 1947). McIlhenny (1932) provided a detailed historical description on how snow geese (*Chen caerulescens*) and

Table 11. Use of unspecified plant parts (1), achenes (2)[a], leaves and shoots (3), and corms and rhizomes (4) of *Scirpus maritimus* and *S. robustus* as food by groups of waterfowl.

Reference	Waterfowl (general)	Dabbling ducks	Diving, sea, and stiff-tailed ducks	Geese and brant	Swans
Scirpus maritimus					
McAtee 1918		1			
Wetmore 1918		2			
Mabbott 1920		2			
Wetmore 1921				2	
Steenis 1939	1				
Addy 1946		2			
Mendall 1949		1			
Yocom 1951		2			
Harris 1952		2			
Spencer 1953		2			
Stirrett 1954				1	
Gillham 1956					1
Keith and Stanislawski 1960		2			
Keith 1961		2	2		
Yocom and Keller 1961		2	2		
Hartman 1963		1			
Gore 1965	2				
Lebret 1965				4	
Gaevskaya 1966				1	
Cronan and Halla 1968		1	1		
Nagel 1969				3,4	
Burgess 1970		2			
Swanson and Bartonek 1970		2			
Fiala and Kvet 1971	3,4				
Kvet and Hudec 1971				3	
Tamisier 1971, cited in Podlejski 1981		2			
Kerwin and Webb 1972		1	1		
Zwarts 1972, cited in Reed 1989				3,4	
Kadlec and Wentz 1974	2				
Loosjes 1974, cited in Reed 1989				3,4	
Ondok and Kvet 1978				1	
Pehrsson 1980		2			
Podlejski 1981, 1982	2				
Duncan and D'Herbes 1982		2			
Pederson and Pederson 1983		2			
Euliss 1984		2			
Smith and Kadlec 1985c				3	
Miller 1987		2			
Euliss and Harris 1987		2			
Pehrsson 1988		2		4	
Hothem and Ohlendorf 1989		2			
Thorn and Zwank 1993		2			
Scirpus robustus					
McAtee 1910				3,4	
Mabbott 1920		2			
McIlhenny 1932				4	
Cottam 1935				3,4	
Addy 1946		2			
Glazener 1946				4	

Table 11. *Continued.*

Reference	Waterfowl (general)	Dabbling ducks	Diving, sea, and stiff-tailed ducks	Geese and brant	Swans
Lynch et al. 1947				4	
Beckwith and Hosford 1956		1			
Beter 1957		2			
Stewart and Manning 1958					2
Kimble 1958		2	2		
Chamberlain 1959	2			2	
Davison and Neely 1959	1				
Yelverton and Quay 1959				2,4	
Neely 1960	2				
Glasgow and Bardwell 1962		2			
Stewart 1962		2			
George 1963		2		3,4	
Bardwell et al. 1965.		2			
George et al. 1965, cited in Mall 1969		2			
Stieglitz 1972		1			
Kadlec and Wentz 1974	2				
Landers et al. 1976		2	2		
Prevost et al. 1978		2			
Beam and Gruenhagen 1980		2			
Connelly and Chesemore 1980		2			
Sandifer et al. 1980	1				
Smith and Odum 1981				1	
Smith, T. 1983				4	
Strange 1987				4	
Stutzenbaker and Weller 1989				3,4	

[a] Achenes may also serve as grit.

whooping cranes (*Grus americana*) extract *S. robustus* rhizomes.

Tundra swans (*Cygnus columbianus*) eat *S. robustus* achenes (Stewart and Manning 1958). Gillham (1956) stated that *S. maritimus* is seldom eaten by mute swans (*C. olor*), although the birds may severely damage stands by trampling.

Other waterbirds use *S. maritimus*, especially American coots, which eat the achenes and leaves and build their nests with the aboveground parts (Jones 1940; Reznicek 1973; Smith and Kadlec 1985c). *Scirpus maritimus* is eaten by long-billed dowitchers (*Limnodromus scolopaceus*; Sperry 1940). Coots and soras (*Porzana carolina*) also feed on *S. robustus* achenes (Webster 1964; Prevost et al. 1978). Passerine species such as long-billed marsh wrens (*Cistothorus palustris*), common yellowthroats (*Geothlypis trichas*), red-winged blackbirds (*Agelaius phoeniceus*), and boat-tailed grackles (*Quiscalus major*) may forage extensively in tidal wetlands where *S. robustus* is a dominant or co-dominant plant (Peterson et al. 1995). Epstein and Joyner (1986) and DeVoe and Baughman (1986) list many other birds that use impoundments containing *S. robustus*.

Mammals

Plants in the genus *Scirpus* are important to mammals (Martin et al. 1951). *Scirpus maritimus* and *S. robustus* are used for food and cover by furbearers, including muskrats and nutria (*Myocastor coypus*; Arthur 1931; Lynch et al. 1947; O'Neil 1949; Harris and Webert 1962; Gaevskaya 1966; Palmisano 1972; Podlejski 1981). Simulated grazing experiments by Taylor (1992) in Louisiana suggested that extreme herbivory by nutria may lower the abundance of *S. robustus*. This bulrush, in mixed stands with *Salicornia virginica*, *Atriplex patula*, and *Frankenia grandifolia*, provides good habitat for the endangered saltmarsh harvest mouse (*Reithrodontomys raviventris*; Shellhammer et al. 1982). Domestic animals including cattle, horses, sheep, and swine also eat these bulrushes (Mall 1969; Zafar 1976; Brehm 1979;

George 1980; Podlejski 1981). Although *Scirpus maritimus* harvested in North Dakota seems distinctly unpalatable to sheep (Christensen et al. 1947), Ranwell (1961) noted an increase in this bulrush in the absence of sheep grazing in *Spartina*-dominated marshes in England. Blankenship (1905, cited in Yanovsky 1936) stated that *Scirpus maritimus* rootstocks are eaten by Amerindians.

Economics

Scirpus maritimus and *S. robustus* have economic values other than those related to fisheries, wildlife, and livestock production. The belowground rhizome systems can stabilize soft, bottom substrates and thus reduce water turbidity (Gillham 1957; Kadlec and Wentz 1974). Stands of *S. maritimus* successfully filter the fecal pathogen *Escherichia coli* from sewage effluent (Seidel 1971). *Scirpus maritimus* may remove phenols from industrial waste and can be used to make paper (Zafar 1976). *Scirpus robustus* pioneers and becomes a prominent plant in constructed wastewater treatment ponds (Gearheart et al. 1984) but probably is less able to take up heavy metals than other common marsh plants (Lee et al. 1976). *Scirpus robustus* is sometimes used in aquatic plant nurseries to reduce temperatures of industrial wastewater (Ailstock 1989) and to treat urban runoff (Meiorin 1989).

The two bulrushes may have yet undiscovered beneficial uses. Some stilbenes extracted from *S. maritimus* increase the life span of cancerous mice, inhibit formation of potato (*Solanum tuberosum*) galls, reduce activity of brine shrimp (*Artemia salina*), decrease feeding activity of fall army worms (*Spodoptera frugiperda*), and inhibit growth of duckweed (*Lemna minor*; Powell et al. 1987). The root (presumably corm) of this bulrush is used in China as an astringent and diuretic (Chopra et al. 1956, cited in Powell et al. 1987).

The economic impact of the two bulrushes can also be negative. *Scirpus maritimus* or closely-related species are noxious weeds in rice fields in at least 10 countries in Europe, Asia, Africa, and the South Pacific (Nakagawa et al. 1973; Kim and De Datta 1974; Visperas and Vergara 1976a; Podlejski 1982; Bernasor and De Datta 1986; Powell et al. 1987). In these fields, *S. maritimus* may compose nearly 30% of the dry weight of weeds (Janiya and Moody 1984) and reduce rice yields by 60-100% (Ampong-Nyarko and De Datta 1991). *Scirpus maritimus* also reduces flow rates of agricultural drainwater in ditches (Batten 1967). *Scirpus robustus* or closely-related speciers are pests in California rice fields (George 1980).

Propagation and Management

Note: Some of the chemicals mentioned in this and the following section may be considered unsafe for application to aquatic environments, and no endorsement of the use of any particular chemical is implied or intended. Readers are hereby advised to strictly adhere to application instructions on pesticide labels formulated by the U.S. Environmental Protection Agency.

Since the early 1930's, impounded coastal wetlands, where *Scirpus robustus* and other hydrophytes are grown for waterfowl food, have been reclaimed from colonial-age rice paddies in the southern and southeastern United States (Tiner 1977; Miglarese and Sandifer 1982; Tompkins 1986). The area of individual management units may exceed 4,000 ha (Sandifer et al. 1980). Similarly, during the late 1800's, cropland and pastures began to be reclaimed from tidally influenced wetlands in California; these efforts largely failed, and, during the 1930's, private hunting clubs began to acquire and manage most of these lands for waterfowl (Mall 1969). Additional interest in the management of *S. robustus* grew from its value to muskrats, especially in Louisiana (Lay and O'Neil 1942).

Common problems with the management of *S. robustus* in impoundments and natural wetlands include the plant's inconsistent achene germination, difficulties with maintenance of proper water levels and timing of annual salinity cycles, and competition from more and less salt-tolerant hydrophytes. Localized problems are acidification of bottom sediments caused by the oxidation of iron polysulfides and conflicts with attempts to control saltmarsh mosquitoes. Research findings and suggestions on how to produce and maintain *S. robustus* published before 1970 (Lay and O'Neil 1942; O'Neil 1949; Myers 1956; Beter 1957; Neely 1958, 1960, 1962; Davison and Neely 1959; Chabreck 1960; Miller 1962; George 1963; Palmisano 1967; Baldwin 1968; Hoffpauer 1968; Palmisano and Newsom 1968; Perkins 1968; Soileau 1968; Chandler 1969) indicate that the following factors are necessary to produce good stands: (1) flat- or nearly flat-bottomed wetlands; (2) achenes seeded in spring at adequate rates by aircraft (large areas) or corms planted 8-15 cm deep (small areas); (3) well-lit environments provided by dry bottoms irrigated with shallow water just prior to seeding, except where acidification of bottom sediments by oxidation of iron polysulfides is a problem; (4) water held 3-8 cm deep for 2-3 weeks during germination, followed by drainage to moist-soil conditions for 2-3 days to prevent wave-action damage to seedlings; (5) water-level management after stand establishment whereby levels are raised to depths of no more than 30 cm and then gradually lowered to moist-soil stage one or more times during the growing season; (6) soil extract or water salinities of about 7-10 g/L; and (7) an absence of introduced plants with similar ecological requirements. Managers attract wintering waterfowl by flooding these wetlands to prescribed depths at appropriate times and intervals.

These earlier studies showed that it is possible to maintain established stands for years with sustained management but that control of undesirable plants may be necessary. Irrigations with freshwater impede upward movement of salts to help reduce competition by halophytes. Further reductions in soil salinity and additional control of competing halophytes often are achieved when water tables are low if wetlands are drained for brief periods to take advantage of salt leaching by spring rainfall. Withdrawals of surface water or irrigations with seawater raise salinities and help control glycophytes. In some areas, two crops of achenes are produced with well-timed irrigations and drainages.

No experiments were conducted on the response of *S. robustus* to livestock grazing in managed impoundments during the pre-1970 period. However, general observations in the southern United States show a favorable response, whereas production in California stands is reduced, especially with summer grazing (Wendell Miller, U.S. Soil Conservation Service, California [retired], personal communication).

In brackish wetlands along the U.S. gulf coast, fire or combinations of fire and tillage in stands of competing emergents promote stands of *S. robustus* that can persist for 2 or 3 years. Such treatments in more saline wetlands may be totally unsuccessful. Managers sometimes reduce amounts of competing plants such as *Spartina patens* with properly timed fires, if climatic and tidal conditions after the burns are favorable. Application of some herbicides to competing emergents also favors this species.

In general, early studies revealed that effective management of *Scirpus robustus* for waterfowl must emphasize improvements to environmental conditions for the species during periods of the reproductive cycle when achene production can be stimulated. These studies also showed that freshening of irregularly flooded salt marshes encourages invasion by *S. robustus* and that tidal fluctuations can increase salinities to control many pest glycophytes.

Later research and reviews of existing programs refined management of *S. robustus* in coastal impoundments in the eastern and southern United States (McNease and Glasgow 1970; Palmisano 1970, 1972; Wilkinson 1970; Morgan 1974; Landers et al. 1976; Morgan et al. 1976; Barko et al. 1977; Heitzman 1978; Prevost and Gresham 1981; Epstein and Baughman 1986; Loesch et al. 1989). Brief summaries of current management practices in these areas are available (Prevost 1987; Gordon et al. 1989; Hindman and Stotts 1989; Payne 1992). Falco and Cali (1977) and Kadlec and Smith (1984) reviewed general establishment techniques for hydrophytes. The South Carolina Sea Grant Consortium (1986, 1987) provided additional management and maintenance recommendations for impoundments that support *S. robustus* communities.

Recent techniques for managing *S. robustus* include complex water-level management and salinity control measures to take advantage of daily tides and discharges over pre-set spillways for better water circulation. Salinities are carefully and frequently monitored and water tables are maintained below bottom surfaces, especially during critical rainfall periods, to prevent proliferation of undesirable emergents. Modern managers of impoundments also consider the needs of animal species other than waterfowl (e.g., penaeid shrimp and transient marine fish) and try to minimize mosquito production (DeVoe et al. 1986).

Currently, a typical management cycle for established stands of *S. robustus* includes: (1) a partial spring drainage for 2-8 weeks to create moist-soil conditions, allowing sprouting of belowground parts and minimizing acidification of bottom substrates; (2) a complete drainage in late spring or early summer to water table depths of 25-46 cm below the bottom surface for 1-2 weeks; (3) an early or midsummer irrigation with 15-20 cm of water; and (4) a slow increase in water depths while maintaining water circulation to maturate achenes for use by waterfowl.

Above- or below-normal rainfall during late spring or early summer frequently necessitates salinity management. Water salinity in wetlands managed for *S. robustus* is usually about 1-20 g/L, whereas wetlands of higher salinity are usually managed for submersed species. Salinity stress caused by summer drought may require that managers switch to production of other plants. Impoundments at the lower end of the salinity range (1-5 g/L) are usually managed without a complete drainage in late spring or early summer. New plantings of *S. robustus* from achenes are made in March on moist bottoms where soluble salts do not exceed 9 ppt. Water levels are raised to no more than 5 cm after seedlings appear. Whole-plant transplants are sometimes used in small areas such as dredge spoils. Transplanting in fall is not recommended because of dormancy in winter.

The later studies of *Scirpus robustus* showed that burning in winter of dense, established stands can greatly increase use of this species by dabbling ducks, especially when managers quickly reflood stands to optimum foraging depths of 10-15 cm. Burning is usually done every 3 years, during mid-November to mid-March, after hard frosts terminate photosynthesis. Burns in November or December encourage feeding by geese and ducks, whereas burns in February or March facilitate trapping of rodents to reduce their damage to dikes. Managers recommend not burning during drought when the salinity of tidal waters is greater than 15 g/L to avoid creating areas devoid of vegetation. Burning of brackish marshes should be combined with water level and salinity management. Burning and tilling established stands of less desirable perennial emergents generally does not result in great increases in the abundance of *S. robustus*. Control of undesirable plants with herbicides is costly and the effects are poorly understood, although Jones and Lehman (1987) noted a great increase in *S. robustus* 2 years after a stand of *Phragmites australis* was fall-treated with glyphosate.

Techniques for managing *S. robustus* were also refined in valley and coastal wetlands of California, where stands are subject to high salinities and large seasonal changes in salinities (Ustin et al. 1982). In these wetlands, rapid growth of *S. robustus* in the spring may increase its competitive advantage over certain halophytes (e.g., *Salicornia*) during summer periods of high salinity. Although growth of the bulrush may cease completely during these periods, corms survive. Maintenance of the normal cycle of low salinity in spring and high salinity in summer may also prevent the encroachment of less salt-tolerant but highly competitive glycophytes such as *Scirpus acutus* and *Typha latifolia*. Studies on natural and impounded wetlands (Rollins 1973; George 1980; Pearcy et al 1982; Ustin et al. 1982; Pearcy and Ustin 1984; [all summarized by Heitmeyer et al. 1989]) show the importance of spring leaching cycles with low-salinity water that is followed by circulation at constant water depths during the growing season. These practices help reduce soil salinity and enhance growing conditions. In other areas, fall flooding may be followed by spring drainage, or a series of spring drainages may be followed by short irrigations in spring or summer or in spring and summer. For established stands in the San Joaquin Valley, Connelly (1979) recommended drainage in March to achieve a 19-21° C bottom substrate temperature for germination of achenes and to stimulate rhizome growth. This is followed by irrigation in May, when flowers are in the pollen stage, to aid achene production. A second irrigation in June helps mature the achenes. Flooding from about October to late March reduces disease potential and plant regrowth and maximizes waterfowl consumption of the achene crop. In summary, management of *S. robustus* in these wetlands must involve maintenance of annual salinity cycles as well as reductions in yearly average salinities.

Much less is known about management of *S. maritimus* than of *S. robustus*, although successful programs to increase populations of the former on Great Plains waterfowl refuges began during the mid-1930's (Steenis 1939). Some *S. maritimus* is managed for waterfowl as far north as Montana, where irrigation return flows provide a water source (Ball et al. 1989). Plantings of this bulrush can revegetate stripmine ponds in the northern Great Plains (Fulton et al. 1983).

Most information on the management of *S. maritimus* is from studies in the Great Basin, northern Europe, and the Camargue, France. Work by Wetmore (1921), Jensen (1940), and Nelson (1954) on impoundments in Utah led to studies by Kaushik (1963), Teeter (1963, 1965), Bolen (1964), Craner (1964), and Nelson and Dietz (1966), who outlined the effects of salinity and other factors on the germination, growth requirements, production, ecology, and waterfowl use of several salt-tolerant plants of known importance as waterfowl foods. Methods to control *Typha*, a serious competitor of *S. maritimus* in these impoundments, were also investigated. Results of these earlier studies are summarized in Christiansen and Low (1970).

More recent investigations improved techniques for the management of *S. maritimus*. O'Neill (1972) developed methods to increase achene germination of California populations and to seed and manage established stands. Currently, many California wetlands are managed for waterfowl plant foods other than *S. maritimus* (Mushet et al. 1992). (Note that plants in these California studies may have been *S. robustus* or *S. glaucus* or *S. maritimus* × *glaucus* hybrids; see the taxonomy and distribution sections).

In Utah, L. Smith (1983), Smith and Kadlec (1983), Kadlec and Smith (1984), Smith et al. (1984), Smith and Kadlec (1985a,b,c,d), and Foote (1988) studied the effects of wetland drainage in combination with burning and haying, how composition of seed banks relates to existing vegetation, and the natural movements of achenes among various vegetation types (findings summarized in Smith and Kadlec [1986] and Kadlec and Smith [1989]).

Investigations in northern European salt marshes and in the Camargue wetlands reveal various aspects of the results of livestock grazing on *S. maritimus* (Pehrsson et al. 1973; Bassett 1980; Britton and Podlejski 1981; Podlejski 1981, 1982; Duncan and D'Herbes 1982; Pehrsson 1988).

A summary of the aforementioned studies indicates that *S. maritimus* readily pioneers on saline bottoms of managed wetlands if water is applied and depths do not exceed 18 cm. Established stands withstand occasional exposure of bottom substrates. Invasion of glycophytes such as *Typha* spp. is probable where conductivities of bottom substrates (1:5 soil suspension) fall below about 6 mS/cm. Drainage of the impoundments for at least 2 years increases salinities and allows *S. maritimus* achenes to germinate and replace the *Typha*. More *S. maritimus* achenes germinate under 4-5 cm of water than on moist soil. Plants that germinate under increased salinity compete with *S. maritimus* in many wetlands. For example, control of the woody halophyte *Tamarix pentandra*, which is common in the western United States, is difficult after stands enter their second growing season. Fortunately, flooded conditions do not allow *T. pentandra* to germinate. Therefore, the most practical water-level management scheme for *S. maritimus* in many areas is alternating drying and reflooding several times during a growing season to keep salinities high enough to discourage glycophytes, while maintaining shallow water during periods when certain competing halophytes are most likely to germinate. Flooding during fall and winter of established stands followed by gradual drainage by midsummer produces good yields of achenes where competition by halophytes is not a problem. In these areas, prolonged flooding in summer results in poor achene production and stands are usually rapidly invaded by *Typha* and other undesirable freshwater plants. In addition, high water levels can increase wave action and decrease survival rates of corms (Foote 1988).

Burning in spring of stands of *S. maritimus* after removal of surface water seems to have little influence on achene production and on the number of germinable achenes in the seed bank. Nevertheless, such fires probably are beneficial because the frequency of plants increases while vegetative reproduction continues. In wetlands of coastal Texas, prescribed burning of *S. maritimus* (probably *S. robustus*, see taxonomy and distribution sections) increases its use by wintering geese (Stutzenbaker and Weller 1989). Mowing with removal of plants (haying) reduces productivity significantly more than burning, probably because of the lack of a nutrient pulse from the ash. Nevertheless, stands may benefit from occasional haying to remove excess vegetation. In northern Europe, mowing of achene-producing stands of *S. maritimus* in September should be followed by an increase in water level (Pehrsson 1988). This practice allows ducks to feed on newly mature achenes and discourages the problem plant *Phragmites australis*.

Cattle and horses readily graze *S. maritimus*, especially young plants. Cattle often consume only the reproductive buds and inflorescences, even at high stocking rates. Heavy grazing can increase corm consumption by geese because these birds are reluctant to enter dense, ungrazed vegetation. However, severe grazing by livestock can greatly reduce the value of affected wetlands to waterfowl that consume achenes. In the French Camargue, *S. maritimus* often remains dominant in wetlands regularly grazed by horses during the growing season; without horses, *Phragmites australis* becomes dominant. Because maximal production of achenes, corms, and herbage of *S. maritimus* cannot be obtained simultaneously in the same area, Pehrsson (1988) proposed alternating cattle grazing and nongrazing on an interval of several years as the best option for wildlife managers in northern Europe. He noted the need, however, for the development of better methods to control *Phragmites australis* where *S. maritimus* may attain high achene production. In some Great Basin wetlands, cattle grazing of stands of *S. maritimus* after mid-July helps maintain the semiopen aspect preferred by feeding or resting waterfowl. In the northern Great Plains, stands of *S. maritimus* may benefit from moderate to heavy grazing and tillage (Pederson et al. 1989). In England, herbicides that kill aboveground but not belowground parts of *S. maritimus* can temporarily control competing emergents (Axell 1982). Regrowth occurs and the bulrush colonizes bare areas formerly occupied by less herbicide-tolerant competitors.

Early attempts by Fischer (1907, cited in Isely 1944) and Martin and Uhler (1939) to obtain high germination rates in *S. maritimus* and *S. robustus* were generally unsatisfactory. Isely (1944) showed that the two species are similar because germination of achenes is extremely poor unless they are after-ripened (stratified) and then exposed to relatively high temperatures (30-32° C) and light during the germination period. Thus, best conditions for good germination in the field probably are shallow, clear, warm water. Achenes of *S. robustus* are highly resistant to deterioration. When submerged, weight loss is only about 1% in 90 days (Neely 1956, 1960, 1962; George 1963). Germinability declines with age of achenes (George and Young 1977) and is highly variable geographically

(George 1980). Fresh achenes of both bulrushes require scarification, stratification, fermentation, and extended periods of soaking or other treatments to assure high germination rates and to prevent achenes from drifting away (Steenis 1939; Christensen et al. 1947; Salyer 1949; Clevering 1995).

Salyer (1949) noted that dry-stored achenes of both bulrushes are prone to weevil infestations and require frequent inspection. He recommended planting rootstocks (rhizomes) to establish stands in relatively stable water. Rootstock removal is easier if stands established from seed are first thinned, mowed, and plowed. To prevent the spread of noxious weeds, Salyer (1949) recommended washing rootstocks to free them of soil and extraneous plant material. Rootstocks are resistant to dry, cold conditions and can be stored under heavy layers of straw or other mulch (Steenis 1939). Managers can also plant substrate cores that contain rhizomes to establish stands of *S. maritimus* (Moody 1978). Transplant sites should not have excessive wave action (Pomeroy et al. 1981). Hoag and Sellers (1994) noted better survival of wild *S. maritimus* plants than of those grown in a greenhouse.

For both bulrushes, germinability of dry achenes can be improved by soaking them in a dilute (1-4%) solution of sodium hypochlorite (common laundry bleach; George 1963; Clevering 1995). However, the treatment may yield inconsistent germination if posttreatment drying is excessive (George and Young 1977; George 1980). O'Neill (1972) successfully seeded *S. maritimus* (possibly including *S. robustus* or "*S. tuberosus*" = *S. glaucus* or various hybrids; see taxonomy and distribution section) after such treatment in combination with a regime of high illumination and temperature. He achieved the regime by holding achenes in an outdoor pit lined with plastic sheeting and covered with transparent film. Achene dormancy is broken in about 12-15 days, after which sowing can begin immediately at 3.4-5.6 kg wet weight/ha on shallowly flooded areas. The most effective procedure is probably moist overwinter storage followed by air-drying in spring just before sowing. Moist achenes stratified for 2-3 months at constant 2° C may yield germination rates as high as 97%. Stratification periods should not exceed 2 years (Clevering 1995). Prevost and Gresham (1981) recommended submersing achenes in polyester bags in brackish impoundments for 45 days. Achenes mixed with clean sand and refrigerated in darkness at 4.5° C for 45 days show even better germination but require more material and equipment. The germination rate of achenes dry-stored for 4 months can reach 80% if the achenes are scarified by immersion in concentrated sulfuric acid for 2 minutes (Dietert and Shontz 1978).

Achenes of both bulrushes can also be pre-germinated (incubated until roots or epicotyls emerge from the achenes) and held in outdoor peat pots until used (Garbisch 1993; Clevering 1995). Clevering (1995) noted higher rates of plant establishment by *S. maritimus* when pre-germinated achenes were buried at 0.5 cm in sediment than when raw achenes were similarly buried or merely sown on the sediment surface. Gloves should be worn when handling these achenes because the awns on their scales frequently penetrate the skin.

Control Methods

Chemical Control

This section is a review of information on attempts to kill *Scirpus maritimus* and *S. robustus* or to control their growth with herbicides.

Scirpus maritimus or closely-related species are difficult to control because of apical bud dormancy and ability to produce numerous corms (Ampong-Nyarko and De Datta 1991). Herbicides can be used in rice fields but may not be readily available or may be too costly for widespread use (Vergara et al. 1977). Additionally, rice planted from seedlings requires different herbicides than sown rice. The most common herbicides used to treat *S. maritimus* and other weeds in rice fields in Italy, France, and the Phillipines are the phenoxypropionics (e.g., fenoprop, mecoprop, and dichlorprop), oxadiazon, bentazon, bensulfuron-methyl, 2,4-D, 2,4,5-T, MCPA, and propanil mixed with phenoxyics (Zanini 1974, cited in Podlejski 1981; Vergara et al. 1977; Bernasor and De Datta 1986). An effective but expensive method to control *S. maritimus* is to stimulate corm sprouting with benzyladenine and then kill topgrowth with selective herbicides (Kim and De Datta 1974). Field drains where *S. maritimus* impedes water flow may be opened with a mixture of paraquat (gramoxone) and dalapon (2,2-Dichloropropionic acid; Batten 1967). Paraquat can control this bulrush, but dalapon kills topgrowth only (Axell 1982; Thomas 1982). In England, openings for waterfowl in dense stands of *S. maritimus* can be made with 1 kg a.i./ha glyphosate sprayed in July (Hanley 1981). Ampong-Nyarko and De Datta (1991) provided additional information on the use of herbicides to control this species. *Scirpus maritumus* and putative *S. glaucus* × *maritimus* hybrids are pests in California rice fields

(Browning et al. 1995), but I found no information on chemical control methods.

Physical and Biological Controls

Reviews of the physical and biological methods used to control *Scirpus maritimus* or closely-related species in rice fields include Vergara et al. (1977) and Ampong-Nyarko and De Datta (1991). Thorough weeding by hand gives good control of the plant but is arduous because of the difficulty of extracting the corms. Also, repeated treatment is necessary. Mechanical plowing and multiple harrowings may be effective, but timing is crucial. Corms quickly resprout and delayed harrowing may separate sprouted corms, break their dormancy, and result in increased rather than decreased populations. Growers find that plowing of rice fields within 20 days after harvest reduces sexual reproduction, buries regenerated shoots, and exposes some corms to the atmosphere. If fields are drained and dried after plowing to dessicate exposed corms and lower germinability, populations of bulrush can be reduced, but this practice may be impractical if another rice crop is to be planted immediately or if rainy conditions develop. Rotations of rice with 3 consecutive years of dry-land crops can eliminate *S. maritimus*.

Cultural methods to control *S. maritimus* include the use of taller and longer duration rice cultivars and the closer spacing of plants to take advantage of the sensitivity of this bulrush to shade. For control of this species in northern European wetlands to improve livestock forage, A. Koridon (personal communication in Brehm 1979) suggested a November underwater mowing followed by one or two cuttings in the following year. I found no information on physical or biological control of *S. robustus*.

Research Needs

I interviewed many wetland managers in the United States who are familiar with *Scirpus maritimus* and *S. robustus*. The importance of the two bulrushes for wildlife was recognized by most managers, and they were confident of their ability to establish and maintain stands of these plants on the lands they manage. However, many of the management techniques currently in use involve costly trial-and-error methods. To help reduce the inefficiency of such methods, managers need information to account for the variability of their observed results.

In several areas, managers have switched their efforts from producing monotypic stands of a few species of waterfowl food plants to growing mixed stands with greater numbers of plant species that attract waterfowl and other marsh or aquatic birds. To meet these goals, some managers have directed their efforts toward thinning stands of the two bulrushes or intermixing bulrush stands with those of other food plants, especially shorter emergents and submersed species. Managers need to know the optimum size and interspersion of areas slated for increased plant diversity and how those areas will respond to current management techniques. Part of the effort to increase diversity of food resources stems from a lack of definitive proof of the digestibility and food value of the bulrush achenes to birds. This suggests the need for more complex food preference studies.

Several managers encouraged more research on the timing and intensity of prescribed burning. This practice opens dense stands and increases availability of achenes to wintering waterfowl, but the pre-burn periods when impoundments must be drained and dried may conflict with shrimp management. In areas subject to land subsidence and rises in sea level, it is vital that such burns do not damage rhizome systems and cause further losses of organic matter vital to marsh accretion. Some managers reported that regulations governing smoke management are making it increasingly difficult to conduct prescribed burns. Research to develop other means of thinning dense stands of the two bulrushes would be beneficial.

Most managers of coastal impoundments, where high-salinity water is usually available, reported few problems controlling undesirable freshwater plants by raising salinities. However, a few salt-tolerant plants (e.g., *Scirpus californicus*, *Spartina cynosuroides*, *Typha angustifolia*, and *Zizaniopsis miliacea*) still pose problems because they respond similarly to practices used to grow *Scirpus robustus*. Closure of these impoundments to the open sea for most of the year for management of this bulrush may negatively affect populations of certain marine fish. This problem is most serious where coastal marshes are disappearing because of subsidence and sea level increases. In other coastal areas the reverse can occur. For example, where freshwaters from diverted rivers push estuarine waters seaward it is difficult for managers to obtain waters of sufficient salinity. Some managers reported wetland damage or degradation from airboats and island construction. Research that must be combined with conservation in many coastal areas.

Water pollution was not identified as a problem on most refuges or hunting areas. However, a few managers expressed a need for increased research on propagation techniques for the two bulrushes where the only available water is small amounts of highly saline irrigation return flows. Research there could involve the selection of highly salt-tolerant strains of the two bulrushes. Some managers speculated that valuable genetic diversity of these bulrushes has been lost after long periods of semidomestication through repeated seeding and harvest.

Managers with the ability to control bottom-substrate salinity and water supplies in inland wetlands were satisfied with current techniques used to propagate *S. maritimus*. In wetlands lacking water-control structures or where interstitial substrate salinities have slowly decreased, research is needed on methods to control the adventive *Typha angustifolia*. This species now dominates many moderately saline wetlands where *S. maritimus* once flourished. These wetlands would be good candidates for research to determine whether the combined effects of natural wetland disturbances such as grazing and burning could restore stands of this bulrush.

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Appendixes

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Appendix A. Co-occurrences of *Scirpus maritimus* s. lat. with other emergent vascular plants.

	Reference[a,b] (no. of species)																	
Species (no. of occurrences)	**1 (34)**	**2 (24)**	**3 (20)**	**4 (18)**	**4 (17)**	**5 (14)**	**6 (14)**	**7 (13)**	**8 (13)**	**9 (12)**	**10 (12)**	**11 (12)**	**8 (12)**	**12 (11)**	**5 (11)**	**13 (11)**	**5 (11)**	**14 (10)**
Scirpus maritimus (81)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Phragmites australis (22)		x								x		x			x			x
Triglochin maritima (15)								x	x	x						x	x	
Eleocharis palustris (14)	x						x			x	x		x	x				
Typha latifolia (12)										x	x	x						
Scirpus acutus (11)										x				x		x		
Atriplex patula (9)							x		x		x							
Scirpus pungens (9)									x							x		
Hordeum jubatum (8)									x		x		x	x				
Scirpus tabernaemontani (8)		x						x										
Aeluropus littoralis (7)		x													x			
Aster tripolium (7)			x			x		x									x	x
Glaux maritima (7)							x	x	x								x	x
Juncus gerardii (7)		x						x									x	
Juncus maritimus (7)		x													x		x	
Plantago maritima (7)						x	x	x									x	
Scirpus validus (7)										x								
Ranunculus sceleratus (6)	x			x	x			x			x							
Epilobium hirsutum (5)	x			x	x													
Polygonum lapathifolium (5)				x	x								x					
Rumex maritimus (5)	x			x	x						x							
Scirpus lacustris (5)												x						
Suaeda depressa (5)									x									
Typha angustifolia (5)		x										x						
Alisma plantago-aquatica (4)	x	x												x				
Atriplex hastata (4)		x		x	x													x
Phalaris arundinacea (4)					x								x					
Puccinellia maritima (4)								x										x
Scolochloa festucacea (4)										x	x							
Typha spp. (4)														x				
Apium graveolens (3)		x				x												
Aster brachyactis (3)									x		x							
Chenopodium rubrum (3)				x							x							
Echinochloa crus-galli (3	x																	
Poa sp. (3)		x		x	x													
Puccinellia nuttalliana (3)									x		x							
Puccinellia phryganodes (3)							x											
Salicornia europaea (3)							x	x										
Salicornia herbacea (3)		x	x												x			
Salicornia rubra (3)									x	x								
Senecio congestus (3)							x		x									
Sonchus asper (3)				x	x													

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	Reference^{a,b} (no. of species)																	
Species (no. of occurrences)	1 (34)	2 (24)	3 (20)	4 (18)	4 (17)	5 (14)	6 (14)	7 (13)	8 (13)	9 (12)	10 (12)	11 (12)	8 (12)	12 (11)	5 (11)	13 (11)	5 (11)	14 (10)
Suaeda maritima (3)		x	x															x
Armeria maritima (2)						x											x	
Artemisia biennis (2)													x	x				
Aster squamatus (2)		x																
Beckmannia syzigachne (2)													x	x				
Butomus umbellatus (2)	x											x						
Carex paleacea (2)							x											
Cirsium arvense (2)				x	x													
Cirsium vulgare (2)				x	x													
Cressa cretica (2)															x			
Cyperus distachyos (2)															x			
Eleocharis acicularis (2)													x					
Epilobium sp. (2)				x	x													
Erigeron canadensis (2)				x					x									
Festuca rubra (2)																	x	
Juncus articulatus (2)	x																	
Limonium spp. (2)						x												
Lycopus europaeus (2)	x																	
Polypogon maritimus (2)		x																
Polypogon monspeliensis (2)															x			
Potentilla reptans (2)	x																	
Ranunculus flammula (2)								x										
Rorippa amphibia (2)												x						
Sagittaria sagittifolia (2)	x											x						
Salicornia sp. (2)																x		
Salsola soda (2)						x												
Schoenus nigricans (2)						x												
Scirpus littoralis (2)		x																
Scirpus olneyi (2)																x		
Solanum dulcamara (2)				x	x													
Sparganium ramosum (2)	x											x						
Spergularia sp. (2)		x																
Spergularia marginata (2)																	x	
Spergularia marina (2)						x												x
Typha angustata (2)	x														x			
Acorus calamus (1)	x																	
Alisma gramineum (1)														x				
Alopecurus aequalis (1)													x					
Arthrocnemum glaucum (1)		x																
Arthyaxon lancifolius (1)	x																	
Aster hesperius (1)													x					
Aster subulatus (1)			x															
Azolla sp. (1)		x																

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Appendix A. *Continued.*

	Reference[a,b] (no. of species)																	
Species (no. of occurrences)	1 (34)	2 (26)	3 (20)	4 (18)	4 (17)	5 (14)	6 (14)	7 (13)	8 (13)	9 (12)	10 (12)	11 (12)	8 (12)	12 (11)	5 (11)	13 (11)	5 (11)	14 (10)
Bidens tripartita (1)	x																	
Callitriche sp. (1)		x																
Carex spp. (1)		x																
Chenopodium album (1)									x									
Cyperus ampressus (1)			x															
Cyperus difformis (1)			x															
Cyperus iria (1)			x															
Cyperus rotundus (1)	x																	
Cyperus serotinus (1)	x																	
Digitaria sanguinalis (1)			x															
Diplachne fusca (1)			x															
Echinochloa spp. (1)																x		
Echinochloa colonam (1)	x																	
Echinochloa hispidula (1)			x															
Eclipta prostrata (1)			x															
Equisetum debile (1)	x																	
Equisetum diffusum (1)	x																	
Fimbristylis longispica (1)			x															
Galium hertifolium (1)	x																	
Glyceria aquatica (1)												x						
Helenium autumnale (1)													x					
Inula crithmoides (1)						x												
Iris pseudoacorus (1)					x													
Juncus bufonius (1)							x											
Juncus decipiens (1)			x															
Juncus subulatus (1)		x																
Kummerowia striata (1)			x															
Lolium sp. (1)				x														
Lotus tenuifolius (1)						x												
Marsilea quadrifolia (1)	x																	
Matricaria inodora (1)				x														
Medicago truncatula (1)						x												
Myosotis sylvatica (1)	x																	
Myriophyllum verticillatum (1)	x																	
Nitraria retusa (1)															x			
Obione portulacoides (1)		x																
Oenanthe fistulosa (1)		x																
Poa annua (1)	x																	
Polygonum amphibium (1)												x						
Polygonum bellardii (1)			x															
Polygonum hydropiper (1)	x																	
Polygonum maritimum (1)						x												

	Reference^{a,b} (no. of species)																	
Species (no. of occurrences)	1 (34)	2 (24)	3 (20)	4 (18)	4 (17)	5 (14)	6 (14)	7 (13)	8 (13)	9 (12)	10 (12)	11 (12)	8 (12)	12 (11)	5 (11)	13 (11)	5 (11)	14 (10)
Polygonum pensylvanica (1)																x		
Polygonum punctatum (1)																x		
Polypogon fugax (1)	x																	
Potentilla anserina (1)							x											
Ranunculus cymbalaria (1)											x							
Ranunculus quelpartensis (1)			x															
Rotala indica (1)	x																	
Rumex conglomeratus (1)			x															
Rumex mexicanus (1)													x					
Sagittaria cuneata (1)														x				
Salicornia radicans (1)		x																
Salicornia stricta (1)																		x
Salix triandra (1)					x													
Salvinia natans (1)												x						
Sambucus nigra (1)					x													
Samolus valerandi (1)						x												
Scirpus fluviatilis (1)														x				
Scirpus holoshoenus (1)						x												
Scirpus nevadensis (1)										x								
Scirpus nipponicus (1)			x															
Scirpus palustris (1)	x																	
Scirpus parvulus (1)								x										
Scirpus robustus (1)																x		
Setaria lutescens (1)			x															
Sium latijugum (1)	x																	
Spartina sp. (1)																		x
Spartina alterniflora (1)																x		
Spartina gracilis (1)										x								
Spartina pectinata (1)										x								
Spergula salina (1)								x										
Spergularia canadensis (1)							x											
Spiranthes sinensis (1)	x																	
Stellaria humifusa (1)							x											
Stellaria media (1)				x														
Tamarix pentandra (1)															x			
Taraxacum sp. (1)					x													
Trifolium repens (1)																	x	
Triglochin palustre (1)							x											
Tussilago farfara (1)				x														
Veronica anagallis (1)	x																	

Appendix A. *Continued.*

	Reference[a,b] (no. of species)																					
Species (no. of occurrences)	15 (10)	16 (10)	17 (10)	18 (10)	19 (10)	20 (10)	21 (9)	22 (9)	23 (9)	5 (9)	24 (9)	25 (8)	26 (8)	15 (8)	27 (8)	20 (8)	28 (7)	4 (7)	29 (7)	30 (7)	32 (7)	32 (6)
Scirpus maritimus	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Phragmites australis				x						x						x				x	x	
Triglochin maritima	x	x			x			x			x			x							x	
Eleocharis palustris	x																		x	x		
Typha latifolia				x				x										x				
Scirpus acutus			x										x									
Atriplex patula							x										x		x			
Scirpus pungens	x							x						x								
Hordeum jubatum			x				x												x			
Aeluropus littoralis										x										x		
Aster tripolium																x						
Distichlis spicata (7)		x					x	x					x				x					
Glaux maritima					x																x	
Juncus gerardii															x						x	
Scirpus validus		x						x														x
Plantago maritima					x																x	
Juncus maritimus		x														x						
Ranunculus sceleratus																		x				
Carex lyngbyei (5)	x	x						x														x
Polygonum lapathifolium													x					x				
Rumex maritimus			x																			
Scirpus lacustris				x					x													
Suaeda depressa							x												x			
Typha angustifolia				x																		
Phalaris arundinacea				x														x				
Puccinellia maritima					x						x											
Apium graveolens																	x					
Aster brachyactis			x																			
Chenopodium rubrum			x																			
Echinochloa crusgalli												x										
Potentilla pacifica (3)	x							x						x								
Sonchus asper																		x				
Potentilla reptans						x																
Agrostis stolonifera (2)					x																	
Carex palacea					x																	
Carex gracilis (2)				x																		
Carex riparia (2)				x																		
Cressa cretica										x												
Cyperus distachyos										x												
Deschampsia cespitosa (2)		x												x								
Eleocharis acicularis			x																			
Equisetum palustre (2)														x								

Species (no. of occurrences)	**Reference[a,b] (no. of species)**																					
	15 (10)	**16 (10)**	**17 (10)**	**18 (10)**	**19 (10)**	**20 (10)**	**21 (9)**	**22 (9)**	**23 (9)**	**5 (9)**	**24 (9)**	**25 (8)**	**26 (8)**	**15 (8)**	**27 (8)**	**20 (8)**	**28 (7)**	**4 (7)**	**29 (7)**	**30 (7)**	**32 (7)**	**32 (6)**
Festuca rubra											x											
Hippuris tetraphylla (2)																						x
Juncus articulatus	x																					
Limonium spp.															x							
Lycopus europaeus											x											
Lythrum salicaria (2)									x													
Polygonum ramosissimum (2)							x												x			
Polypogon monspeliensis										x												
Puccinellia palustris (2)																x						
Ranunculus flammula									x													
Schoenus nigricans											x											
Scirpus littoralis																				x		
Sparganium erectum (2)				x																		
Spergularia sp.															x							
Spergularia marginata											x											
Typha domingensis (2)													x				x					
Agrostis alba		x																				
Agropyron pungens (1)						x																
Agrostis exarata (1)								x														
Agrostis palustris (1)	x																					
Agrostis semiverticillata (1)														x								
Agrostis stolonifera																					x	
Allium vineale (1)						x																
Armeria sp. (1)															x							
Arthrocnemum fruticosum (1)																x						
Asparagus acutifolius (1)						x																
Aster sp. (1)															x							
Astragalus glycyphyllos (1)						x																
Atriplex argentea (1)							x															
Atriplex latifolia (1)					x																	
Baldellia ranunculoides (1)																				x		
Carex extensa (1)											x											
Carex nigra (1)									x													
Carex pluriflora (1)																						x
Carex pseudocyperus (1)									x													
Chenopodium glaucum (1)			x																			
Chenopodium murale (1)														x								
Cochlearia officinalis (1)					x																	
Echinochloa glabrescens (1)												x										
Eleocharis sp. (1)																						x
Elymus triticoides (1)													x									
Festuca arundinacea (1)	x																					
Galium palustre (1)									x													

Appendix A. *Continued.*

	Reference[a,b] (no. of species)																					
Species (no. of occurrences)	15 (10)	16 (10)	17 (10)	18 (10)	19 (10)	20 (10)	21 (9)	22 (9)	23 (9)	5 (9)	24 (9)	25 (8)	26 (8)	15 (8)	27 (8)	20 (8)	28 (7)	4 (7)	29 (7)	30 (7)	32 (7)	32 (6)
Glyceria maxima (1)				x																		
Halimione portulacoides (1)											x											
Heliotropium curassavicum (1)							x															
Hydrocotyle vulgaris (1)									x													
Imperata cylindrica (1)										x												
Ipomoea triloba (1)												x										
Juncus littoralis (1)						x																
Juncus textilis (1)													x									
Kochia scoparia (1)			x																			
Leptochloa fascicularis (1)																			x			
Lilaeopsis occidentalis (1)		x																				
Limonium serotinum (1)																x						
Macroptilium lathyroides (1)												x										
Monochoria vaginalis (1)												x										
Oenanthe aquatica (1)																		x				
Oryza sativa (1)												x										
Osmorhiza occidentalis (1)	x																					
Panicum capillare (1)			x																			
Paspalum distichum (1)													x									
Paspalum vaginatum (1)																				x		
Plantago sp. (1)															x							
Poa arida (1)							x															
Polygonum kitaibelianum (1)					x																	
Polypogon viridis (1)						x																
Puccinellia sp. (1)															x							
Salicornia virginica (1)																	x					
Scirpus californicus (1)																	x					
Scirpus cernuus (1)		x																				
Silene inflata (1)						x																
Sonchus maritimus (1)						x																
Spartina maritima (1)																x						
Spergularia diandra (1)										x												
Suaeda baccatax (1)										x												
Veronica scutellata (1)									x													
Zea mays (1)												x										

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Appendix A. *Continued.*

	Reference[a,b] (no. of species)																						
Species (no. of occurrences)	**33 (6)**	**34 (6)**	**35 (6)**	**36 (6)**	**8 (5)**	**5 (5)**	**37 (5)**	**38 (5)**	**39 (5)**	**40 (5)**	**33 (5)**	**41 (5)**	**42 (4)**	**43 (4)**	**44 (4)**	**8 (4)**	**45 (4)**	**46 (4)**	**47 (4)**	**48 (4)**	**49 (4)**	**33 (4)**	**20 (4)**
Scirpus maritimus	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Phragmites australis	x	x		x			x					x						x					
Triglochin maritima														x			x						
Eleocharis palustris			x															x	x				
Typha latifolia		x										x				x							
Scirpus acutus		x					x			x		x				x							
Atriplex patula					x															x			
Scirpus pungens		x												x									
Hordeum jubatum																				x			
Scirpus tabernaemontani	x					x		x															
Aeluropus littoralis				x							x												x
Aster tripolium								x															
Distichlis spicata							x			x													
Scirpus validus																	x		x				
Juncus maritimus	x																					x	
Plantago maritima								x															
Carex lyngbyei														x									
Epilobium hirsutum				x									x										
Scirpus lacustris																	x	x					
Suaeda depressa					x															x			
Typha angustifolia	x											x											
Scolochloa festucacea																x			x				
Typha spp.							x																
Echinochloa crusgalli	x																						
Puccinellia lucida (3)															x						x		
Puccinellia nuttalliana					x																		
Puccinellia phryganodes															x						x		
Salicornia europaea																						x	
Salicornia rubra					x																		
Senecio congestus															x								
Equisetum palustre						x																	
Hippuris tetraphylla																					x		
Lythrum salicaria											x												
Salsola soda																						x	
Scirpus olneyi										x													
Sparganium erectum			x																				
Aster squamatus				x																			
Carex gracilis			x																				
Carex riparia			x																				
Polypogon maritimum				x																			
Rorippa amphibia			x																				
Salicornia sp.		x																					

Appendix A. *Continued.*

	Reference[a,b] (no. of species)																						
Species (no. of occurrences)	33 (6)	34 (6)	35 (6)	36 (6)	8 (5)	5 (5)	37 (5)	38 (5)	39 (5)	40 (5)	33 (5)	41 (5)	42 (4)	43 (4)	44 (4)	8 (4)	45 (4)	46 (4)	47 (4)	48 (4)	49 (4)	33 (4)	20 (4)
Arthrocnemum perenne (1)																							x
Baumea juncea (1)									x														
Blysmus compressus (1)						x																	
Cochlearia anglica (1)						x																	
Eleocharis latiglumis (1)													x										
Eleocharis rostellata (1)										x													
Gahnia trifida (1)									x														
Juncus kraussii (1)									x														
Plantago major (1)													x										
Puccinellia palustris																							x
Rumex crispus (1)											x												
Scorzonera parviflora (1)								x															
Sonchus sp. (1)											x												
Typha orientalis (1)									x														

Appendix A. *Continued.*

Species (no. of occurrences)	**Reference[a,b] (no. of species)**																	
	8 (3)	**50 (3)**	**51 (3)**	**52 (3)**	**53 (3)**	**54 (3)**	**55 (3)**	**5 (3)**	**5 (3)**	**56 (3)**	**57 (3)**	**58 (3)**	**59 (3)**	**60 (3)**	**61 (2)**	**62 (2)**	**63 (2)**	**64 (2)**
Scirpus maritimus	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Phragmites australis		x	x					x	x				x	x				
Triglochin maritima										x								
Eleocharis palustris	x															x		
Typha latifolia		x					x								x			
Scirpus acutus							x											
Atriplex patula										x								
Scirpus pungens					x						x							
Scirpus tabernaemontani								x	x					x				
Juncus gerardii												x						x
Scirpus validus											x							
Alisma plantago-aquatica	x																	
Puccinellia lucida				x														
Typha spp.													x					
Carex subspathacea (1)				x														
Cyperus textilus (1)						x											x	
Juncus spp. (1)			x															
Sparganium sp. (1)					x													
Spartina patens (1)												x						
Triglochin elongatum (1)						x												

[a] References: (1) Handoo and Kaul 1982; (2) Molinier and Tallon 1974, cited in Podlejski 1981; (3) Kim 1971; (4) Reinink and van der Toorn 1975; (5) Chapman 1974; (6) Riley and McKay1980; (7) Klavestad 1957; (8) Walker and Coupland 1970; (9) Metcalf 1931; (10) Walker 1965; (11) Korelyakova 1971; (12) Barker and Fulton 1979; (13) Wright et al. 1949; (14) Ranwell 1961; (15) Forbes 1972, cited in Hoos and Packman 1974; (16) Frenkel and Boss 1988; (17) Stewart and Kantrud 1971; (18) Krahulec et al. 1987; (19) Vevle 1985; (20) Ferrari et al. 1985; (21) Ungar 1965; (22) Hutchinson 1982; (23) Waters and Ferry 1989; (24) Diaz and Fernandez 1989; (25) Bernasor and DeDatta 1986; (26) Schuler 1987; (27) Rees 19[illegible]5, cited in Chapman 1974; (28) Ferren 1985; (29) Ungar 1967; (30) Grillas and Duncan 1986; (31) Jerling 1983; (32) Vince and Snow 1984; (33) Britton and Podlejski 1981; (34) Hammer et al. 1975; (35) Krahulec et al. 1980; (36) Bassett 1978; (37) Jensen 1940, cited in Craner 1964; (38) Hejny and Husak 1978; (39) Congdon 1981; (40) Bolen 1964; (41) Robel 1961; (42) Van Noordwijk-Puijk et al. 1979; (43) Moody 1978; (44) Ewing and Kershaw 1986; (45) Shay and Shay 1986; (46) Jepsen 1970; (47) Smeins 1965; (48) Ungar et al. 1969; (49) Glooshenko and Martini 1987; (50) Kollman and Wali 1976; (51) Coetzer 1987; (52) Martini et al. 1979; (53) Daborn 1975; (54) Millard and Scott 1953; (55) Kadlec and Smith 1984; (56) Dahl and Hadac 1941, cited in Chapman 1974; (57) Ewing 1986; (58) Jacobson and Jacobson 1989; (59) Fiala and Kvet 1971; (60) Duncan and D'Herbes 1982; (61) Olson 1979; (62) Price et al. 1988; (63) Shubert 1982; (64) Hyer 1963.

[b] Same references indicate different study areas or community types; transect data used only in cases where single vegetative zones were sampled and when no obvious elevational gradients were present; lists taken from some community types are from sample plots where *S. maritimus* had highest frequency or cover values. Except for a few common North American species, e.g. *Phragmites australis* (synonym= *P. communis*), no attempt has been made to eliminate synonyms.

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Appendix B. Co-occurrences of *Scirpus robustus* s. lat. with other emergent vascular plants.

	Reference[a,b] (no. of species)																	
Species (no. of occurrences)	**1 (35)**	**2 (23)**	**3 (21)**	**4 (15)**	**5 (14)**	**6 (14)**	**7 (14)**	**8 (11)**	**9 (11)**	**10 (10)**	**11 (9)**	**9 (9)**	**12 (8)**	**13 (8)**	**9 (8)**	**14 (7)**	**2 (6)**	**15 (6)**
Scirpus robustus (34)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Distichlis spicata (20)	x	x		x		x		x	x		x	x		x	x	x	x	x
Spartina alterniflora (18)	x	x			x		x	x	x	x		x	x	x	x	x	x	x
Scirpus olneyi (13)	x	x	x	x	x		x	x		x				x			x	
Spartina patens (13)		x	x			x		x	x		x	x		x				x
Spartina cynosuroides (12)	x		x		x		x	x	x			x			x	x		
Eleocharis parvula (8)	x			x		x	x	x				x			x			
Juncus roemerianus (8)	x		x			x	x	x	x		x							
Typha angustifolia (8)		x		x	x							x	x		x			x
Pluchea purpurascens (6)					x				x		x	x			x			
Scirpus validus (6)	x													x	x	x	x	
Atriplex patula (5)		x		x	x													
Panicum virgatum (5)	x	x	x										x					
Fimbristylis castanea (4)	x					x								x				
Scirpus pungens (4)						x				x								x
Iva frutescens (4)	x	x			x				x									
Acnida cannabina (3)		x											x					
Cyperus spp. (3)			x			x		x										
Echinochloa walteri (3)	x				x						x							
Eleocharis spp. (3)	x					x										x		
Hibiscus moscheutos (3)		x																
Panicum spp. (3)						x	x		x									
Phragmites australis (3)	x				x			x										
Sagittaria lancifolia (3)			x														x	
Solidago sempervirens (3)		x	x										x					
Baccharis halimifolia (2)	x	x																
Borrichia frutescens (2)	x							x										
Cotula coronopifolia (2)				x														
Cyperus odoratus (2)	x										x							
Cyperus strigosus (2)									x			x						
Ipomoea sagittata (2)	x		x															
Lythrum lineare (2)	x																	
Pluchea camphorata (2)	x					x												
Polygonum pensylvanicum (2)		x								x								
Polygonum punctatum (2)			x							x								
Salicornia europaea (2)									x									
Salicornia virginica (2)				x														
Scirpus acutus (2)				x						x								
Setaria glauca (2)	x		x															
Typha spp. (2)							x									x		
Acer rubrum (1)		x																
Acnida alabamensis (1)	x																	

Species (no. of occurrences)	Reference[a,b] (no. of species)																	
	1 (35)	2 (23)	3 (21)	4 (15)	5 (14)	6 (14)	7 (14)	8 (11)	9 (11)	10 (10)	11 (9)	9 (9)	12 (8)	13 (8)	9 (8)	14 (7)	2 (6)	15 (6)
Alternanthera spp. (1)							x											
Amaranthus cannabinus (1)					x													
Andropogon virginicus (1)		x																
Aster lateriflorus (1)			x															
Aster sp. (1)	x																	
Aster subulatus (1)		x	x															
Bacopa monnieri (1)	x																	
Bacopa rotundifolia (1)	x																	
Calystegia sepium (1)			x															
Chenopodium murale (1)				x														
Cuscuta indecora (1)	x																	
Cynodon spp. (1)						x												
Cyperus filicinus (1)											x							
Echinochloa crus-galli (1)						x												
Echinochloa spp. (1)							x											
Eleocharis albida (1)											x							
Eleocharis halophila (1)													x					
Eleocharis macrostachya (1)			x															
Erechtites hieraciifolia (1)		x																
Gerardia maritima (1)	x																	
Heliotropium curassavicum (1)	x																	
Juncus halophilus (1)													x					
Juniperus virginiana (1)		x																
Kosteletzkya spp. (1)						x												
Kosteletzkya virginica (1)	x																	
Leersia oryzoides (1)			x															
Leptochloa fascicularis (1)	x																	
Limonium carolinianum (1)		x																
Liquidambar styraciflua (1)		x																
Mikania scandens (1)			x															
Panicum dichotomiflorum (1)							x											
Panicum hemitomon (1)			x															
Panicum scoparium (1)			x															
Paspalum vaginatum (1)	x																	
Peltandra virginica (1)					x													
Pinus taeda (1)		x																
Pluchea camphorata (1)		x																
Polygonum aviculare (1)				x														
Polygonum hydropiperoides (1)					x													
Polygonum lapathifolium (1)				x														
Polypogon monspeliensis (1)				x														
Salicornia spp. (1)										x								
Scirpus californicus (1)														x				

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Appendix B. *Continued.*

	Reference[a,b] (no. of species)																	
Species **(no. of occurrences)**	**1 (35)**	**2 (23)**	**3 (21)**	**4 (15)**	**5 (14)**	**6 (14)**	**7 (14)**	**8 (11)**	**9 (11)**	**10 (10)**	**11 (9)**	**9 (9)**	**12 (8)**	**13 (8)**	**9 (8)**	**14 (7)**	**2 (6)**	**15 (6)**
Scirpus maritimus (1)										x								
Sesbania exaltata (1)	x																	
Sesuvium portulacastrum (1)	x																	
Sesuvium verrucosum (1)				x														
Spartina bakeri (1							x											
Spartina spartinae (1)	x																	
Spergularia marina (1)				x														
Teucrium canadense (1)					x													
Triglochin maritimum (1)										x								
Vigna luteola (1)			x															
Vigna repens (1)	x																	
Zizaniopsis miliacea (1)							x											

Appendix B. *Continued.*

	Reference[a,b] (no. of species)															
***Species* (no. of occurrences)**	**16 (6)**	**17 (5)**	**18 (5)**	**19 (5)**	**20 (4)**	**21 (4)**	**9 (4)**	**22 (4)**	**23 (3)**	**24 (3)**	**25 (3)**	**26 (3)**	**27 (3)**	**28 (2)**	**29 (2)**	**30 (2)**
Scirpus robustus	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Distichlis spicata	x	x		x		x	x			x			x			
Spartina alterniflora	x	x		x										x		
Sartina patens	x	x				x				x						
Spartina cynosuroides			x	x			x									
Scirpus olneyi				x				x					x			
Eleocharis parvula											x					
Typha angustifolia							x									
Juncus roemerianus																x
Pluchea purpurascens						x										
Scirpus validus			x													
Atriplex patula					x			x								
Fimbristylis castanea			x													
Panicum virgatum									x							
Scirpus pungens			x													
Acnida cannabina								x								
Hibiscus moscheutos	x								x							
Cotula coronopifolia					x											
Salicornia europaea		x														
Lythrum lineare	x															
Salicornia virginica												x				
Sagittaria lancifolia															x	
Typha domingensis (2)					x						x					
Spartina foliosa (1)												x				

[a] References: (1) Chabreck 1972; (2) Bourn and Cottam 1950; (3) Taylor 1992; (4) Mall 1969; (5) Jones and Lehman 1987; (6) Smith, T. 1983; (7) Landers et al. 1976; (8) Palmisano 1970; (9) Wilkinson 1970; (10) Wright et al. 1949; (11) Waits 1967; (12) Johnson and Raup 1947; (13) Lynch et al. 1947; (14) Kelley and Porcher 1986; (15) Florschutz 1959; (16) Flowers 1973; (17) Linthurst and Seneca 1980; (18) Baden et al. 1975; (19) Palmisano and Newsom 1968; (20) Zedler and Beare 1986; (21) Reimold 1977; (22) Cottam et al. 1938; (23) De Jong and Drake 1981; (24) Soileau 1968; (25) Neely 1960; (26) Pearcy and Ustin 1984; (27) Joanen and Glasgow 1966; (28) Newling et al. 1983; (29) Cruz 1974; (30) Tiner 1977.

[b] Same references indicate different study areas or community types; transect data used only in cases where single vegetative zones were sampled and when no obvious elevational gradients were present; lists taken from some community types are from sample plots where *S. robustus* had highest frequency or cover values. Except for a few common species, e.g. *Phragmites australis* (synonym = *P. communis*), no attempt has been made to eliminate synonyms.

A list of current *Information and Technology Reports* follows:

1 Population Biology of the Florida Manatee, edited by Thomas J. O'Shea, Bruce B. Ackerman, and H. Franklin Percival. 1995. 287 pp.

2 Effects of Fire on Threatened and Endangered Plants: An Annotated Bibliography, by Amy Hessl and S. Spackman. 1995. 55 pp.

3 Pine Plantations and Wildlife in the Southeastern United States: An Assessment of Impacts and Opportunities, by Arthur W. Allen, Yvonne K. Bernal, and Robert J. Moulton. 1996. 32 pp.

4 Aerial Surveys of Waterbirds in Alaska 1957-94: Population Trends and Observer Variability, by John L. Hodges, James G. King, Bruce Conant, and Henry A. Hanson. 1996. 24 pp.

5 An Ecological Framework for Monitoring Sustainable Management of Wildlife: A New Mexico Furbearer Example, by Bruce C. Thompson, Damien F. Miller, Theresa A. Doumitt, Theresa R. Jacobson, and Melody L. Munson-McGee. 1996. 37 pp.

NOTE: The mention of trade names does not constitute endorsement or recommendation for use by the Federal Government.

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U.S. Department of the Interior
National Biological Service

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This responsibility includes fostering the sound use of our lands and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities.

March 3, 1849

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END

09-23-97